ONTOGENETIC SHIFTS IN DIET AND HABITAT BY JUVENILE GREEN SEA TURTLES (*Chelonia mydas*) ALONG THE MIDDLE AND LOWER TEXAS COAST

A Thesis

by

LYNDSEY NICOLE HOWELL

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

August 2012

Major Subject: Wildlife and Fisheries Sciences

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Approved by:

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ABSTRACT

Ontogenetic Shifts in Diet and Habitat by Juvenile Green Sea Turtles (*Chelonia mydas*) along the Middle and Lower Texas Coast. (August 2012)

Lyndsey Nicole Howell, B.S., Texas A&M University at Galveston

Chair of Advisory Committee: Dr. André M. Landry, Jr.

Effective population management of green sea turtles (*Chelonia mydas*) necessitates understanding the temporal variation in foraging grounds used in ontogenetic stages, and the effect that the assimilated diet within those habitats has on nutritional gain, growth and eventual reproductive output. Texas coastal waters provide foraging grounds critical to meeting the nutritional needs of green turtles during early life history. To characterize temporal shifts in foraging strategy stomach contents combined with stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes of scute tissue were examined across size classes of stranded juvenile green turtles from the middle and lower Texas coast during 2007-2010. Findings from dietary analysis generally corroborated those from stable isotopes in scute samples. Results indicate green sea turtles exhibit multiple shifts in diet and habitat along the Texas coast. Although isotope values in the tissues of some <25 cm SCL turtles signified recent recruitment to jetty habitat, most in this size class exhibited depleted $\delta^{13}C$ and enriched $\delta^{15}N$ values indicative of oceanic life. Reinforcing oceanic occupancy from stable isotope results was

forage material dominated by oceanic items such as *Sargassum* spp., *Scyphozoa* spp., and plastic debris. Diet analysis of 25-34.9 cm SCL turtles implied regional differences existed in macroalgae and seagrass consumption. Enriched $\delta^{13}C$ and $\delta^{15}N$ values in newest scute suggest most turtles inhabited the jetty environment, where macroalgae is the most available forage. A definitive shift by >35 cm SCL turtles to inshore seagrass habitat was revealed by a diet of seagrasses and tissue enriched in $\delta^{13}C$ and depleted in $\delta^{15}N$. This is the first study to integrate stomach contents of several green turtle size classes with tissue analysis of stable isotopes. The combination of these techniques provided an assessment of the effectiveness of stable isotope analyses in documenting diet and habitat shifts. Stomach content examination determined the most recent diet consumed within the habitat occupied, whereas stable isotope analysis provided a time-integrated synopsis of diet and habitat shifts. Findings indicate integration of stomach content and stable isotope analysis is highly effective for characterizing habitat use and foraging strategy of ontogenetic-stage green sea turtles.

DEDICATION

For my parents George and Patricia Howell, they have always believed in me and provided the encouragement I needed to succeed. Also to my fiancé, Tim Berk, who supported me immensely throughout this process.

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Furthermore I want to extend my gratitude to Dr. Roger Zimmerman at the National Marine Fisheries Service Lab in Galveston for his constant encouragement and for admittance into the federal student career experience

program. Also I would like to thank Dr. Jason Curtis from the University of Florida's Stable Isotope Lab in the Department of Geology in Gainesville, Fl., who ran all of the stable isotope analyses.

Additionally, I would like to thank the Wildlife and Fisheries Sciences and Marine Biology Department for financial support in the form of graduate teaching assistantships and mini grants. Also thank you to the wonderful people in the graduate offices of both departments that aided me greatly in the graduate process.

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CHAPTER I

INTRODUCTION

Green turtles (*Chelonia mydas*) are listed as threatened throughout their range, with the exception of breeding populations in Florida and along the Pacific coast of Mexico which are listed as endangered (NMFS & USFWS 2007). The 2010 BP Deepwater Horizon oil spill in the Gulf of Mexico (GOM) served to demonstrate that scientists could not predict ecological consequences and effects on key species, such as the green turtle, because many GOM populations had not been adequately assessed (Bjorndal et al. 2011, Campagna et al. 2011). Federal agencies tasked with supervising the recovery of protected species such as the green sea turtle require comprehensive data to assess population dynamics in order to design management strategies to address environmental abuses prior to the next crisis. Anthropogenic threats to green turtles include ingestion of, and entanglement in, plastic debris (McCauley & Bjorndal 1999); incidental capture in commercial and recreational fisheries (National Research Council 1990); and habitat degradation (Seminoff et al. 2002, Santos et al. 2011). Research findings must be constantly integrated into conservation strategies to facilitate species survival (Meylan & Ehrenfeld 2000). Identifying important marine foraging habitats, as well as evaluating the extent of ingestion of marine debris, are priorities of the recovery plan for the Atlantic

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This thesis follows the style of Marine Ecological Progress Series.

green turtle in preventing an irreversible decline in this species (NMFS & USFWS 1991). Despite decades of management, green turtle populations have not recovered, leading many to question current stock assessments and the biological data used in population models. Strategic management of sea turtle populations, in part, mandates research to define the degree of variation in diet at diverse foraging grounds and the effect that diet assimilation has on net nutritional gain, growth, and, ultimately, reproductive output (Bjorndal 1985).

Size-based dietary shifts have been documented for a variety of fauna and are often associated with habitat transferences (Werner & Gilliam 1984). The freshwater turtle *Trachemys scripta* has been recognized as switching from a chiefly carnivorous diet when young to a predominantly herbivorous diet abruptly at 60 mm plastron length (Clark & Gibbons 1969). An individual may shift to a different foraging habitat when its current trophic resource fails to sustain growth (Forseth et al. 1999, Morinville & Rasmussen 2003). Upon leaving the nesting beach, hatchling green turtles enter the oceanic realm where they forage as opportunistic omnivores for up to 10 years (Carr & Meylan 1980, Carr 1987, Zug et al. 2002, Reich et al. 2007) before transitioning to neritic developmental habitats at approximately 25 - 40 cm straight carapace length (SCL) (Coyne 1994, Shaver 1994, Musick & Limpus 1997).

Scientists have historically applied gut content analyses, fecal examination and stomach lavage techniques to define sea turtle foraging dynamics (Bjorndal 1980, Coyne 1994). Recently, analysis of stable isotopes of

nitrogen ($^{15}N/^{14}N$, $\delta^{15}N$) and carbon ($^{13}C/^{12}C$, $\delta^{13}C$) retained in tissues is being used to resolve sea turtle foraging dynamics (Hatase et al. 2002, Reich et al. 2007, Arthur et al. 2008, Caut et al. 2008, Reich et al. 2010). Elemental isotopes are assimilated from the turtle's diet into its tissues and consequently each tissue retains that isotope value over a period of time (average residence time), thus allowing the use of stable isotope analysis to assess the history of an animal's diet (DeNiro & Epstein 1978, 1981). Using $\delta^{13}C$ and $\delta^{15}N$, Reich et al. (2007) described the habitat and diet for post-hatchling to juvenile green turtles, indicating that stable isotope analysis can be used instead of the more invasive stomach lavage technique to effectively examine the foraging habits of sea turtles.

Historically, large numbers of green turtles supported a commercial fishery in Texas, with annual landings exceeding 265,000 kg that, over time, decimated the resident turtle assemblage (Doughty 1984, Witzell 1994). Recently, directed-capture initiatives (Metz and Landry unpublished, Shaver 2000) and data collected during hypothermic cold stunning events (Shaver 2012) have documented exponential increases in Texas' juvenile green turtle population. Mark-recapture data collected from 1991 to 2011 suggest that Texas provides the largest neritic developmental foraging grounds west of the Mississippi River (Metz and Landry unpublished). Anecdotal observations and in-water mark-recapture data indicate juveniles, primarily <50 cm SCL, occupy Texas' jetty channel passes (Renaud et al. 1995, Shaver 2000) while turtles >30

cm SCL occupy seagrass beds of coastal bays (Coyne 1994, Renaud et al. 1995, Arms 1996). Although in-water research (Shaver 2000, Metz and Landry unpublished), behavioral observations (Shaver 1994) and stomach lavage (Coyne 1994) have documented green turtles migrating between these two distinct habitats, only stable isotope analysis has illustrated an ontogenetic shift from jetty environment to seagrass pastures with a subsequent diet change (Gorga 2010). Characterizing foraging strategies of Texas' juvenile green turtle assemblage is fundamental to understanding patterns of this species' survivorship, as most inhabitants are likely from breeding populations in the GOM (Shaver 2000). Comprehensive information on diet and nutrients assimilated in this critical foraging zone is deficient for all size ranges of green turtles residing on the Texas coast.

Research described herein utilized stomach content and stable isotope analyses to characterize the feeding habits of several size classes of juvenile green turtles occupying coastal waters of the middle (MTC) and lower Texas coast (LTC). The aim of this research was to apply both analyses, combined by individual turtle, to better define ontogenetic shifts and foraging habits of green turtles occupying jetty and bay regions in Texas. In addition, the efficacy of stable isotope analysis was assessed as a less invasive and more efficient technique in defining foraging habits of green sea turtles.

CHAPTER II

DIET AND HABITAT SHIFTS OF GREEN SEA TURTLES INVESTIGATED THROUGH STOMACH CONTENT ANALYSIS

INTRODUCTION

Marine turtle researchers have utilized stranded turtles to elucidate foraging dynamics while concurrently examining temporal, sex-specific diet, and size-class trends (Work & Balazs 2002, Ferreira et al. 2006, Seney & Musick 2007, Russell & Balazs 2009). The National Marine Fisheries Service has oversight of marine protected species and uses data from the Sea Turtle Stranding and Salvage Network (STSSN) to support formulation of species-wide management decisions. Integration of diet studies with associated STSSN data on distribution, morphometrics, and gross necropsy findings, is vital to managing the conservation and recovery of marine turtles. Investigating gastrointestinal tract contents for the presence of oceanic and neritic diet taxa offers the prospect of determining life history stage (Van Nierop 1984) while additionally illustrating resource partitioning within size ranges (Shaver 1994, López-Mendilaharsu et al. 2005).

Bjorndal (1997) reported that when a juvenile green turtle's diet shifts from omnivorous to herbivorous, the digestive system requires time to allow for hindgut microbial adaptation. Green turtles consuming a low-quality diet rely on hindgut microbial fermentation for a significant energy source (Bjorndal 1979). A

mixed diet of seagrass and algae may have lower nutritional value with subsequent nutrient gain maximized by the ability to ingest a greater quantity (Bjorndal 1997). Primary-diet taxa consumed by green turtles vary geographically: Phaeophyta and Chlorophyta algae are most commonly ingested in Oman (Ferreira et al. 2006); in Kane'ohe Bay, Hawaii, Rhodophyta algae are the main diet component (Russell & Balazs 2009); seagrass spp. dominate the green turtle diet in the Caribbean (Bjorndal 1980, Mortimer 1981). Terrestrial plant material, as well as animal matter, has also been described as an essential component of neritic green turtles' diet in the Pacific (Limpus 2000, Russell et al. 2011).

Jetty passes provide critical routes for sea turtle movement between the GOM and adjacent bay systems (Coyne 1994, Shaver 1994), with juvenile green turtle residency at Texas channel passes documented at ≤ 1100 days (Shaver 2000). In-water research in Texas documented that green turtles netted in channels had consumed mainly algae while larger turtles captured in bay systems had foraged primarily on seagrasses (Landry et al. 1992, Coyne 1994, Shaver unpubl. data). It is assumed that turtles < 25 cm SCL in this study will have a diet indicative of an omnivorous oceanic stage. New recruits to the neritic zone, 25 to 34.9 cm SCL, will reveal a diet of predominantly macroalgae that would have been consumed off of jetty structures. Larger juveniles, >35 cm SCL, will have ingested a diet primarily of seagrasses from within the bay systems. The jetty and seagrass beds are important in the developmental stage

of green turtles; therefore, it is critical to collect detailed diet descriptions of the size classes utilizing these habitats.

MATERIALS AND METHODS

Study Area. Stranded turtles were recovered from the Texas coastal bend region south to the Texas border, STSSN zones 19-21 (Fig. 1), which includes the following major bay systems: Matagorda Bay, San Antonio Bay, Aransas Bay, Corpus Christi Bay and the Laguna Madre. Differences in benthic marine communities and seagrass bed composition in Texas warranted assessment of regional differences in green turtle diet between the middle Texas coast (MTC) (STSSN zone 19 and partial of zone 20) and lower Texas coast (LTC) (STSSN 21 and majority of zone 20) (Fig. 2). Mud and sand bottoms characterize the nearshore zone with limited artificial reefs present offshore in state waters (<9 nm). High-energy navigable waterways into the bay systems are lined with rock jetties that facilitate tidal flow, protect channel entrances from wave action and reduce sediment accretion. Benthic marine communities of macroalgae and invertebrates exist along these jetties, with seasonal and locational fluxes in density and concentration (Hicks & Tunnell 1995, Kaldy et al. 1995, Renaud et al. 1995, Fikes & Lehman 2008). Seagrass beds are unevenly distributed among Texas' bay systems as a result of suspended sediments, anthropogenic activities, variable precipitation, and freshwater discharge dynamics (Pulich & Onuf 2007). Eighty percent of seagrass beds in Texas occur in the hypersaline Laguna Madre (Pulich 1999, Tunnell & Judd 2002), where

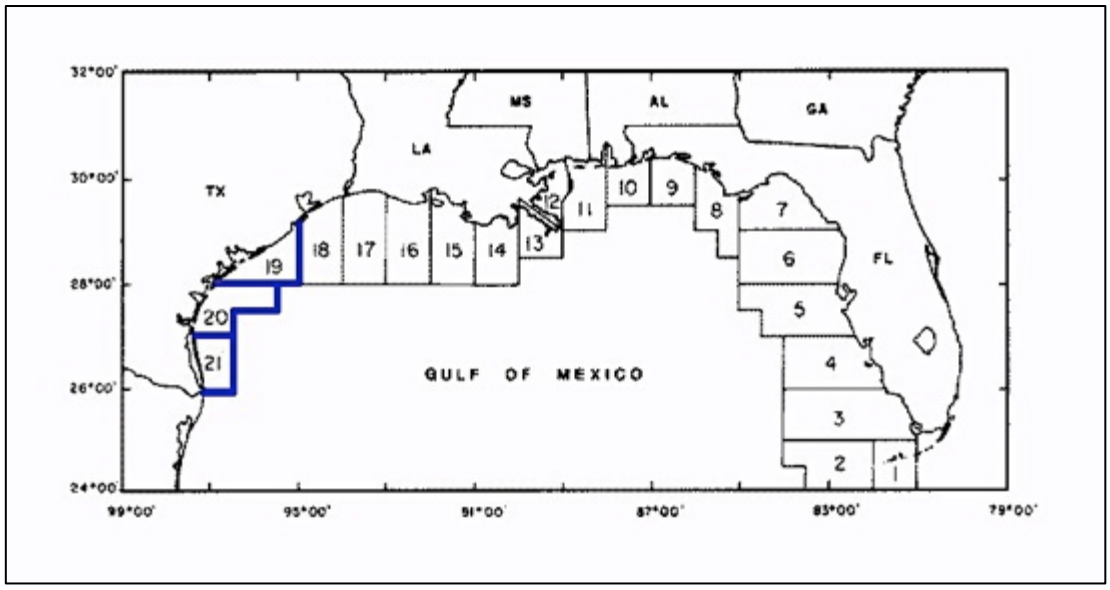


Figure 1. Sea Turtle Stranding and Salvage Network Statistical Zones. Highlighted zones 19-21 yielded stranded green sea turtles analyzed in this study.

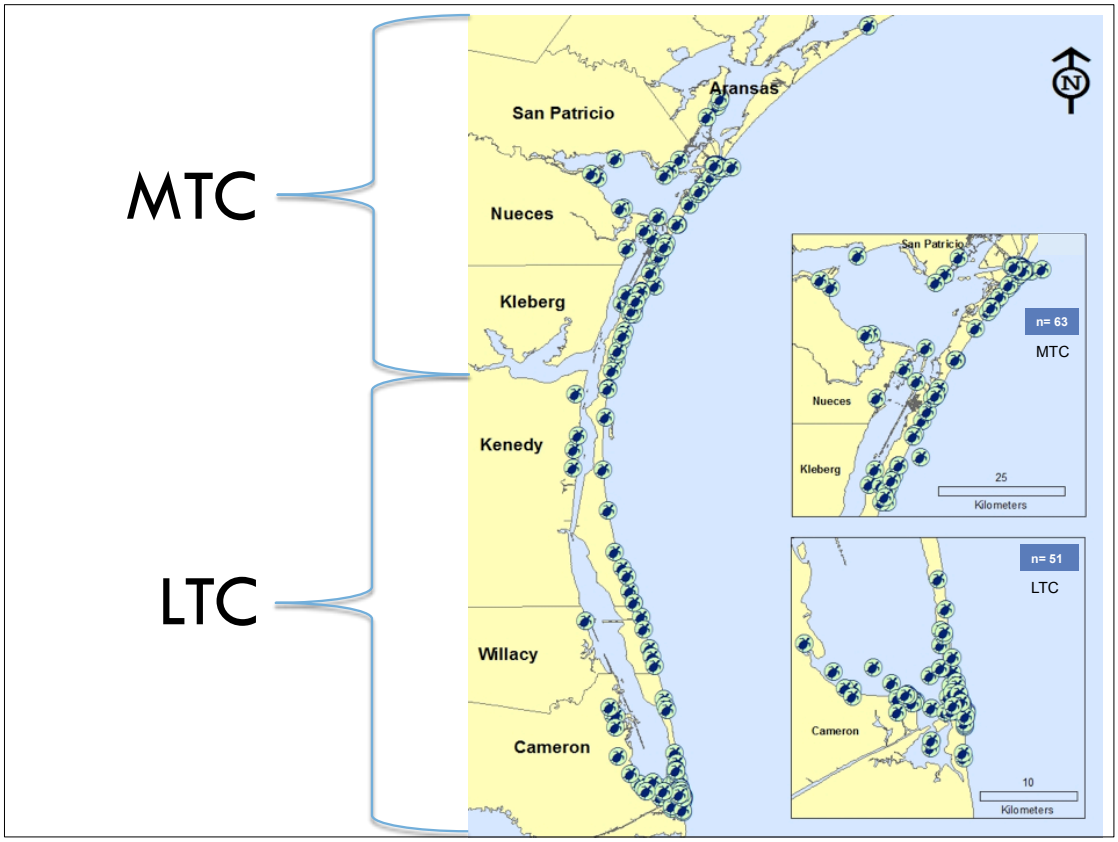


Figure 2. Juvenile green sea turtle stranding locations along the middle (MTC) and lower Texas coast (LTC) that were analyzed in this study.

common species include shoal grass (*Halodule wrightii*), manatee grass (*Syringodium filiforme*), and turtle grass (*Thalassia testudinum*) (Quammen & Onuf 1993, Withers 2002).

Sample Collection. Green turtle carcasses used in examining diet across early life history stages were collected from 2007-2010 from offshore (Gulf waters or beach shoreline) and inshore (bays, channels, or respective shoreline) stranding locations within the study area. Collection was restricted to turtles that had recently stranded dead, did not exhibit signs of long-term illness (Bjorndal et al. 1994), and were classified as STSSN code 1 (fresh dead) or 2 (slightly decomposed). Stranded carcasses were inspected following sampling procedures developed by the STSSN to generate morphometric data and gross necropsy findings. All measurements presented are straight carapace length (SCL), measured from carapace notch to posterior tip. The entire length of the digestive tract was removed from each carcass during necropsy investigation and frozen for subsequent analysis.

Diet Data Collection. Significant degradation of ingested food in the hindgut occurs as digestive enzymes break down complex carbohydrates and proteins that vary between algae and seagrass species (Bjorndal 1979). Therefore, characterization of diet items was restricted to the foregut (i.e., esophagus and stomach) where digestion is minimal and items could then be identified to the lowest possible taxon with a dissecting microscope. Esophagus and stomach contents analyzed were combined and are collectively referred to

as stomach contents hereafter. Recovered dietary items were identified to the lowest possible taxon with a dissecting microscope. Volumetric analysis (to the nearest 0.1 ml) of stomach content taxa was applied using water displacement in a graduated cylinder following the technique described by Wolfert and Miller (1978).

Data Analysis. Data were examined in 10-cm size classes to assess potential differences within the following size ranges: 15-24.9, 25-34.9, 35-44.9, 45-54.9, and >55 cm SCL (Fig. 3). Limited numbers of large juvenile green turtles strand along the Texas coast; subsequently, all sizes of turtles >55 cm SCL were combined for analysis.

Diet Descriptions. Percent volume by individual diet taxon (*V*ind) was calculated by dividing the volume of each diet taxon in a given turtle by the total volume of that turtle's stomach contents (x 100). The relative importance of each item in the diet of green turtles was determined using an index of relative importance (IRI; Bjorndal 1997):

$$\% \text{ IRI} = [100(FiVi)] / \Sigma(FiVi)$$

where *F* is the frequency of occurrence of the target taxon *i*, and *V* is the mean percent taxon volume in all individual turtles (*V*ind). The IRI is a compound index that incorporates frequency of occurrence and volume into a single numerical measure to provide a better estimate of dietary importance.

Regional Diet Comparison. Statistical analyses were conducted using IBM SPSS 19.0 statistical software. Data were tested for normality; Levene's

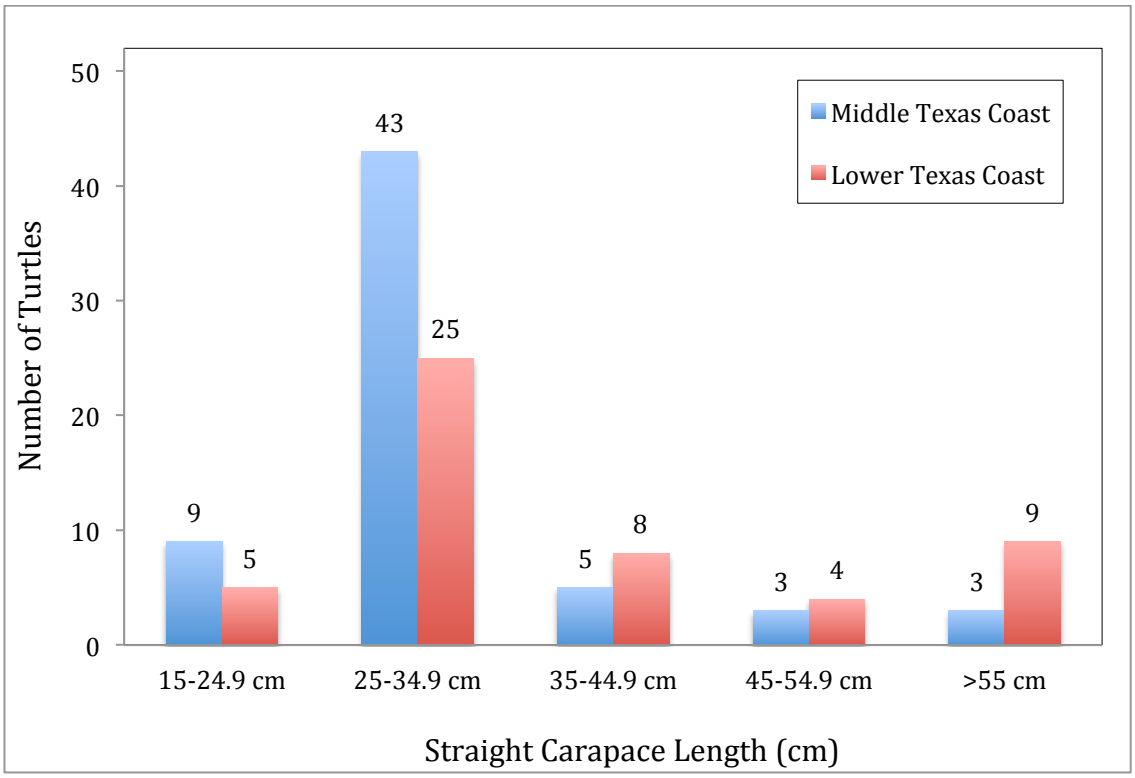


Figure 3. Straight carapace length (cm) frequency of stranded green sea turtles used in analyses. Stranding locations were along the middle and lower Texas coast during 2007-2010. Sample size is listed above the bar for each size class.

test was used to test for homogeneity of variances, and a Welch ANOVA was applied to allow for unequal variances. Volume percentages were log transformed to promote normality for statistical analyses. A comparative histogram figure was created for both regions to analyze how the contribution of relative principal diet items (F ≥25%) varied among the 10-cm size classes (Fig. 4). Differences in consumption of principal diet components among the five size classes of green turtles stranded within each sampling region were examined with a one-way ANOVA. A multiple pairwise comparison test was utilized when ANOVA was significant to explore between group differences. Diet consumed within the same size class for each region was compared with a Students t-test to demonstrate any regional differences.

RESULTS

Diet Description. Stomach contents were examined from 114 green turtles, resulting in a combined total volume of 6475.8 ml. Mean SCL of turtles from MTC was 31.5 cm (SE= 1.18, Range = 17.6-65.4 cm, n = 63) while that for counterparts from LTC was 37.9 cm (SE= 1.78, Range = 15.5-69.6 cm, n = 51). Mean stomach sample volume from the MTC was 36.7 ml (SE = 4.80, Range = 0.8-166.2 ml) compared to 81.7 ml (SE = 21.86, Range = 1.0-959.0 ml) for LTC turtles. Juvenile green turtles consumed a variety of items (Tables 1-5). Five major prey groups were identified based on taxa frequently observed (F ≥25%) within the size classes: Anthophyta, Rhodophyta, Phaeophyta, Chlorophyta, and animal matter. The % IRI values for gut contents of juvenile

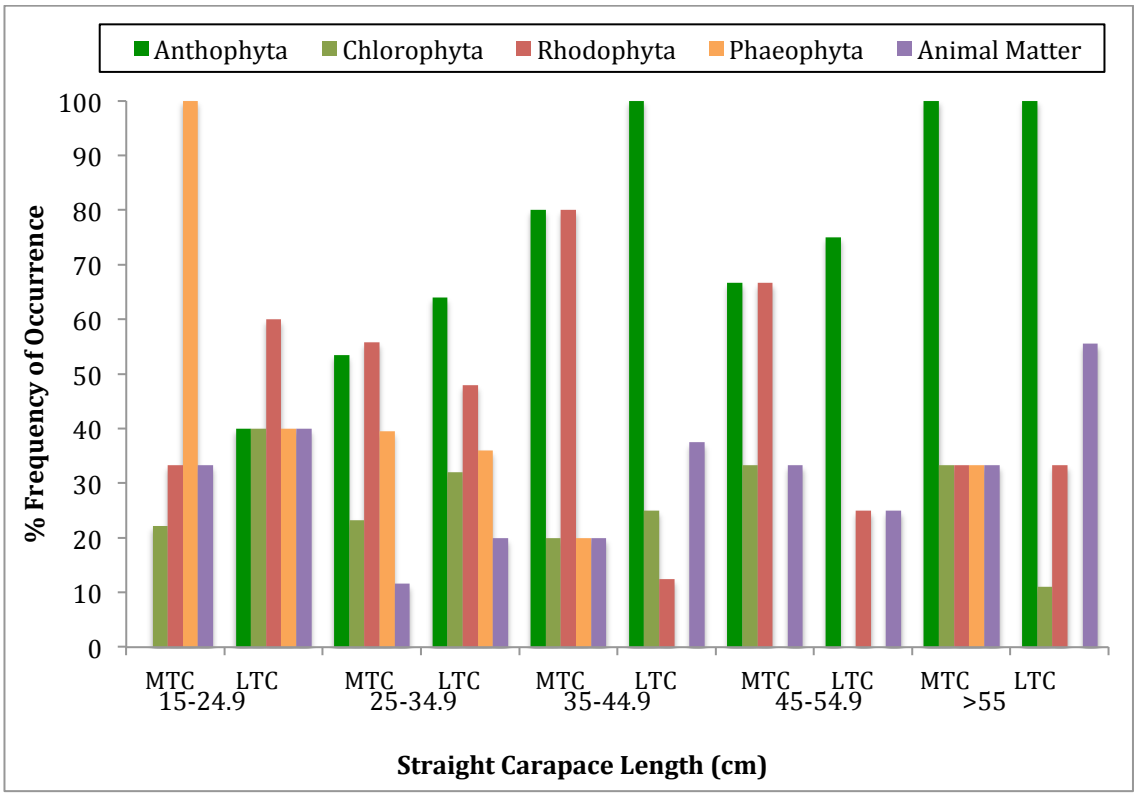


Figure 4. Frequency of occurrence of major (F >25%) diet items consumed by each size class of juvenile green sea turtles stranding along the middle and lower Texas coast during 2007-2010.

Table 1. Percent occurrence (% F), percent volume by individual (% Vind) and percent index of relative importance (% IRI) of prey items in stomachs of 15-24.9 cm SCL green sea turtles stranding along the middle (MTC) and lower Texas coast (LTC) during 2007-2010. % Vind is the total volume for each diet item consumed by all turtles in the region.

	MTC			LTC		
Diet Item	**% F**	**% Vind**	**% IRI**	**% F**	**% Vind**	**% IRI**
Anthophyta	**0.00**	**0.00**	**0.00**	**40.00**	**97.65**	**46.21**
Halodule wrightii	0.00	0.00	0.00	40.00	4.67	2.34
Halophila decipens	0.00	0.00	0.00	0.00	0.00	0.00
Halophila engelmannii	0.00	0.00	0.00	0.00	0.00	0.00
Syringodium filiforme	0.00	0.00	0.00	40.00	82.61	41.28
Thalassia testudinum	0.00	0.00	0.00	20.00	10.36	2.59
Chlorophyta	**22.22**	**25.19**	**2.80**	**40.00**	**13.71**	**3.43**
Caulerpa mexicana	0.00	0.00	0.00	0.00	0.00	0.00
Chaetomorpha gracilis	0.00	0.00	0.00	0.00	0.00	0.00
Cladophora albida	0.00	0.00	0.00	0.00	0.00	0.00
Codium taylorii	0.00	0.00	0.00	20.00	0.20	0.05
Halimeda incrassata	0.00	0.00	0.00	0.00	0.00	0.00
Ulva fasciata	11.11	22.99	2.56	0.00	0.00	0.00
Ulva lactuca	11.11	2.20	0.24	20.00	13.51	3.38
Rhodophyta	**33.00**	**123.66**	**18.25**	**60.00**	**83.78**	**20.94**
Aglaothamnion halliae	11.11	0.66	0.07	0.00	0.00	0.00
Centrocerus clavulatum	11.11	11.01	1.22	0.00	0.00	0.00
Ceramium subtile	0.00	0.00	0.00	0.00	0.00	0.00
Digenea simplex	0.00	0.00	0.00	0.00	0.00	0.00
Gelidium crinale	22.22	40.60	9.02	20.00	40.54	10.13
Gracilaria cervicornis	0.00	0.00	0.00	20.00	5.18	1.29
Gracilaria tikvahiae	0.00	0.00	0.00	0.00	0.00	0.00
Grateloupia filicina	11.11	11.49	1.28	0.00	0.00	0.00
Halymenia floridana	0.00	0.00	0.00	0.00	0.00	0.00
Hydropuntia caudata	0.00	0.00	0.00	20.00	8.33	2.08
Hypnea musciformis	11.11	1.54	0.17	0.00	0.00	0.00
Hypnea spinella	0.00	0.00	0.00	0.00	0.00	0.00
Jania capillacea	0.00	0.00	0.00	20.00	2.70	0.68
Laurencia obtusa	11.11	57.47	6.39	0.00	0.00	0.00

Table 1 Continued

	MTC			LTC		
Diet Item	**% F**	**% Vind**	**% IRI**	**% F**	**% Vind**	**% IRI**
Lomentaria baileyana	0.00	0.00	0.00	0.00	0.00	0.00
Polysiphonia denudata	0.00	0.00	0.00	0.00	0.00	0.00
Pterocladiella bartlettii	11.11	0.44	0.05	20.00	13.51	3.38
Rhodymenia psuedopalmata	0.00	0.00	0.00	20.00	13.51	3.38
Spyridia filamentosa	11.11	0.44	0.05	0.00	0.00	0.00
Phaeophyta	**100.00**	**166.76**	**59.64**	**40.00**	**59.69**	**25.66**
Dictyota menstrualis	0.00	0.00	0.00	0.00	0.00	0.00
Hincksia mitchelliae	22.22	79.21	17.61	0.00	0.00	0.00
Padina gymnospora	0.00	0.00	0.00	0.00	0.00	0.00
Rosenvingea orientalis	11.11	6.61	0.73	0.00	0.00	0.00
Sargassum fluitans	55.56	47.92	26.62	40.00	43.02	17.21
Sargassum natans	44.44	33.02	14.68	20.00	16.67	19.33
Animal Matter	**33.00**	**77.47**	**11.45**	**40.00**	**15.07**	**3.77**
Phylum Porifera	0.00	0.00	0.00	0.00	0.00	0.00
Class Scyphozoa	22.22	25.63	5.69	0.00	0.00	0.00
Diopatra cupera	0.00	0.00	0.00	0.00	0.00	0.00
Family Penaeidae	0.00	0.00	0.00	0.00	0.00	0.00
Infraorder Brachyura	11.11	5.75	0.64	0.00	0.00	0.00
Class Bivalvia	11.11	5.00	0.56	20.00	13.51	2.70
Class Gastropoda	0.00	0.00	0.00	20.00	1.55	0.31
Class Ophiuroidea	0.00	0.00	0.00	0.00	0.00	0.00
Infraclass Teleostei	11.11	41.10	4.57	0.00	0.00	0.00
Other	**55.56**	**14.15**	**7.86**	**0.00**	**0.00**	**0.00**
Anthropogenic Debris	55.56	14.15	7.86	0.00	0.00	0.00
Terrestrial Plant Matter	0.00	0.00	0.00	0.00	0.00	0.00

Table 2. Percent occurrence (% F), percent volume by individual (% Vind) and percent index of relative importance (% IRI) of prey items in stomachs of 25-34.9 cm SCL green sea turtles stranding along the middle (MTC) and lower Texas coast (LTC) during 2007-2010. % Vind is the total volume for each diet item consumed by all turtles in the region.

	MTC			LTC		
Diet Item	**% F**	**% Vind**	**% IRI**	**% F**	**% Vind**	**% IRI**
Anthophyta	**53.48**	**125.23**	**20.90**	**64.00**	**190.24**	**53.48**
Halodule wrightii	34.88	48.61	16.96	24.00	16.25	3.9
Halophila decipens	2.33	1.82	0.04	0.00	0.00	0.00
Halophila engelmannii	4.65	7.96	0.37	8.00	56.15	4.49
Syringodium filiforme	2.33	57.38	1.33	40.00	66.57	26.63
Thalassia testudinum	23.26	9.46	2.20	36.00	51.26	18.46
Chlorophyta	**23.26**	**108.46**	**6.31**	**32.00**	**88.19**	**8.20**
Caulerpa mexicana	0.00	0.00	0.00	0.00	0.00	0.00
Chaetomorpha gracilis	2.33	2.11	0.05	0.00	0.00	0.00
Cladophora albida	2.33	20.00	0.47	0.00	0.00	0.00
Codium taylorii	0.00	0.00	0.00	4.00	66.67	2.67
Halimeda incrassata	2.33	4.76	0.11	0.00	0.00	0.00
Ulva fasciata	4.65	65.33	3.04	8.00	5.66	0.45
Ulva lactuca	16.28	16.26	2.65	32.00	15.87	5.08
Rhodophyta	**55.80**	**514.63**	**43.98**	**48.00**	**154.19**	**21.46**
Aglaothamnion halliae	0.00	0.00	0.00	0.00	0.00	0.00
Centrocerus clavulatum	2.33	8.33	0.19	0.00	0.00	0.00
Ceramium subtile	2.33	18.52	0.43	0.00	0.00	0.00
Digenea simplex	4.65	33.53	1.56	8.00	9.09	0.73
Gelidium crinale	25.58	65.92	16.86	24.00	39.67	9.52
Gracilaria cervicornis	0.00	0.00	0.00	0.00	0.00	0.00
Gracilaria tikvahiae	4.65	60.19	2.80	0.00	0.00	0.00
Grateloupia filicina	13.95	45.25	6.31	8.00	46.67	3.73
Halymenia floridana	2.33	98.43	2.29	0.00	0.00	0.00
Hydropuntia caudata	11.63	14.46	1.68	4.00	8.20	0.33
Hypnea musciformis	6.98	43.53	3.04	12.00	1.38	0.17
Hypnea spinella	2.33	6.17	0.14	0.00	0.00	0.00
Jania capillacea	0.00	0.00	0.00	4.00	2.44	0.10
Laurencia obtusa	6.98	29.1	2.03	12.00	6.33	0.76

Table 2 Continued

	MTC			LTC		
Diet Item	**% F**	**% Vind**	**% IRI**	**% F**	**% Vind**	**% IRI**
Lomentaria baileyana	0.00	0.00	0.00	0.00	0.00	0.00
Polysiphonia denudata	2.33	26.47	0.62	0.00	0.00	0.00
Pterocladiella bartlettii	9.30	64.74	6.02	20.00	28.23	5.65
Rhodymenia psuedopalmata	0.00	0.00	0.00	4.00	12.20	0.49
Spyridia filamentosa	0.00	0.00	0.00	0.00	0.00	0.00
Phaeophyta	**39.53**	**150.93**	**24.31**	**36.00**	**64.20**	**9.63**
Dictyota menstrualis	0.00	0.00	0.00	12.00	13.05	1.57
Hincksia mitchelliae	2.33	32.35	0.75	4.00	6.67	0.27
Padina gymnospora	4.65	1.85	0.09	4.00	10.79	0.43
Rosenvingea orientalis	2.33	5.17	0.12	0.00	0.00	0.00
Sargassum fluitans	20.93	61.34	12.84	24.00	30.09	7.22
Sargassum natans	20.93	50.21	10.51	4.00	3.60	0.14
Animal Matter	**11.63**	**49.62**	**2.15**	**20.00**	**78.50**	**4.90**
Phylum Porifera	0.00	0.00	0.00	4.00	14.85	0.59
Class Scyphozoa	9.30	9.18	0.85	4.00	15.38	0.62
Diopatra cupera	0.00	0.00	0.00	4.00	4.29	0.17
Family Penaeidae	0.00	0.00	0.00	0.00	0.00	0.00
Infraorder Brachyura	0.00	0.00	0.00	0.00	0.00	0.00
Class Bivalvia	4.65	15.44	0.72	8.00	6.46	0.52
Class Gastropoda	2.33	25.00	0.58	0.00	0.00	0.00
Class Ophiuroidea	0.00	0.00	0.00	0.00	0.00	0.00
Infraclass Teleostei	0.00	0.00	0.00	8.00	37.51	3.00
Other	**27.91**	**10.88**	**2.35**	**16.00**	**43.56**	**2.34**
Anthropogenic Debris	27.91	7.18	2.00	16.00	4.94	0.79
Terrestrial Plant Matter	9.30	3.70	0.34	4.00	38.63	1.55

Table 3. Percent occurrence (% F), percent volume by individual (% Vind) and percent index of relative importance (% IRI) of prey items in stomachs of 35-44.9 cm SCL green sea turtles stranding along the middle (MTC) and lower Texas coast (LTC) during 2007-2010. % Vind is the total volume for each diet item consumed by all turtles in the region.

	MTC			LTC		
Diet Item	**% F**	**% Vind**	**% IRI**	**% F**	**% Vind**	**% IRI**
Anthophyta	**80.00**	**160.00**	**56.47**	**100.00**	**131.90**	**95.34**
Halodule wrightii	20.00	3.95	0.79	12.50	4.05	0.51
Halophila decipens	0.00	0.00	0.00	25.00	11.20	2.80
Halophila engelmannii	0.00	0.00	0.00	0.00	0.00	0.00
Syringodium filiforme	20.00	94.86	18.97	62.50	40.03	25.01
Thalassia testudinum	60.00	61.19	36.71	87.50	76.61	67.02
Chlorophyta	**20.00**	**4.00**	**0.80**	**25.00**	**24.32**	**3.04**
Caulerpa mexicana	0.00	0.00	0.00	12.50	24.32	3.04
Chaetomorpha gracilis	0.00	0.00	0.00	0.00	0.00	0.00
Cladophora albida	0.00	0.00	0.00	0.00	0.00	0.00
Codium taylorii	0.00	0.00	0.00	0.00	0.00	0.00
Halimeda incrassata	0.00	0.00	0.00	0.00	0.00	0.00
Ulva fasciata	0.00	0.00	0.00	0.00	0.00	0.00
Ulva lactuca	20.00	4.00	0.80	0.00	0.00	0.00
Rhodophyta	**80.00**	**96.00**	**23.06**	**12.50**	**0.40**	**0.05**
Aglaothamnion halliae	0.00	0.00	0.00	0.00	0.00	0.00
Centrocerus clavulatum	0.00	0.00	0.00	0.00	0.00	0.00
Ceramium subtile	0.00	0.00	0.00	0.00	0.00	0.00
Digenea simplex	0.00	0.00	0.00	0.00	0.00	0.00
Gelidium crinale	20.00	96.00	19.20	12.50	0.20	0.02
Gracilaria cervicornis	0.00	0.00	0.00	0.00	0.00	0.00
Gracilaria tikvahiae	0.00	0.00	0.00	0.00	0.00	0.00
Grateloupia filicina	0.00	0.00	0.00	0.00	0.00	0.00
Halymenia floridana	0.00	0.00	0.00	0.00	0.00	0.00
Hydropuntia caudata	60.00	0.00	3.86	0.00	0.00	0.00
Hypnea musciformis	0.00	0.00	0.00	0.00	0.00	0.00
Hypnea spinella	0.00	0.00	0.00	0.00	0.00	0.00
Jania capillacea	0.00	0.00	0.00	0.00	0.00	0.00
Laurencia obtusa	0.00	0.00	0.00	0.00	0.00	0.00

Table 3 Continued

	MTC			LTC		
Diet Item	**% F**	**% Vind**	**% IRI**	**% F**	**% Vind**	**% IRI**
Lomentaria baileyana	0.00	0.00	0.00	12.50	0.20	0.02
Polysiphonia denudata	0.00	0.00	0.00	0.00	0.00	0.00
Pterocladiella bartlettii	0.00	0.00	0.00	0.00	0.00	0.00
Rhodymenia psuedopalmata	0.00	0.00	0.00	0.00	0.00	0.00
Spyridia filamentosa	0.00	0.00	0.00	0.00	0.00	0.00
Phaeophyta	**20.00**	**83.05**	**16.61**	**0.00**	**0.00**	**0.00**
Dictyota menstrualis	0.00	0.00	0.00	0.00	0.00	0.00
Hincksia mitchelliae	0.00	0.00	0.00	0.00	0.00	0.00
Padina gymnospora	0.00	0.00	0.00	0.00	0.00	0.00
Rosenvingea orientalis	0.00	0.00	0.00	0.00	0.00	0.00
Sargassum fluitans	20.00	83.05	16.61	0.00	0.00	0.00
Sargassum natans	0.00	0.00	0.00	0.00	0.00	0.00
Animal Matter	**20.00**	**15.25**	**3.05**	**37.50**	**12.60**	**1.57**
Phylum Porifera	0.00	0.00	0.00	12.50	8.39	1.05
Class Scyphozoa	0.00	0.00	0.00	0.00	0.00	0.00
Diopatra cupera	0.00	0.00	0.00	12.50	4.05	0.51
Family Penaeidae	20.00	15.25	3.05	0.00	0.00	0.00
Infraorder Brachyura	0.00	0.00	0.00	0.00	0.00	0.00
Class Bivalvia	0.00	0.00	0.00	0.00	0.00	0.00
Class Gastropoda	0.00	0.00	0.00	12.50	0.16	0.02
Class Ophiuroidea	0.00	0.00	0.00	0.00	0.00	0.00
Infraclass Teleostei	0.00	0.00	0.00	0.00	0.00	0.00
Other	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
Anthropogenic Debris	0.00	0.00	0.00	0.00	0.00	0.00
Terrestrial Plant Matter	0.00	0.00	0.00	0.00	0.00	0.00

Table 4. Percent occurrence (% F), percent volume by individual (% Vind) and percent index of relative importance (% IRI) of prey items in stomachs of 45-54.9 cm SCL green sea turtles stranding along the middle (MTC) and lower Texas coast (LTC) during 2007-2010. % Vind is the total volume for each diet item consumed by all turtles in the region.

	MTC			LTC		
Diet Item	**% F**	**% Vind**	**% IRI**	**% F**	**% Vind**	**% IRI**
Anthophyta	**66.67**	**61.03**	**26.47**	**75.00**	**110.20**	**70.25**
Halodule wrightii	66.67	18.38	12.25	0.00	0.00	0.00
Halophila decipens	33.33	5.88	1.96	0.00	0.00	0.00
Halophila engelmannii	33.33	1.47	0.49	0.00	0.00	0.00
Syringodium filiforme	33.33	5.88	1.96	50.00	49.61	24.80
Thalassia testudinum	33.33	29.41	9.80	75.00	60.59	45.44
Chlorophyta	**33.33**	**1.47**	**0.49**	**0.00**	**0.00**	**0.00**
Caulerpa mexicana	0.00	0.00	0.00	0.00	0.00	0.00
Chaetomorpha gracilis	0.00	0.00	0.00	0.00	0.00	0.00
Cladophora albida	0.00	0.00	0.00	0.00	0.00	0.00
Codium taylorii	0.00	0.00	0.00	0.00	0.00	0.00
Halimeda incrassata	0.00	0.00	0.00	0.00	0.00	0.00
Ulva fasciata	0.00	0.00	0.00	0.00	0.00	0.00
Ulva lactuca	33.33	1.47	0.49	0.00	0.00	0.00
Rhodophyta	**66.67**	**51.47**	**34.31**	**25.00**	**100.00**	**25.00**
Aglaothamnion halliae	0.00	0.00	0.00	0.00	0.00	0.00
Centrocerus clavulatum	0.00	0.00	0.00	0.00	0.00	0.00
Ceramium subtile	0.00	0.00	0.00	0.00	0.00	0.00
Digenea simplex	0.00	0.00	0.00	0.00	0.00	0.00
Gelidium crinale	0.00	0.00	0.00	0.00	0.00	0.00
Gracilaria cervicornis	0.00	0.00	0.00	0.00	0.00	0.00
Gracilaria tikvahiae	0.00	0.00	0.00	0.00	0.00	0.00
Grateloupia filicina	0.00	0.00	0.00	0.00	0.00	0.00
Halymenia floridana	0.00	0.00	0.00	0.00	0.00	0.00
Hydropuntia caudata	66.67	51.47	34.31	25.00	100.00	25.00
Hypnea musciformis	0.00	0.00	0.00	0.00	0.00	0.00
Hypnea spinella	0.00	0.00	0.00	0.00	0.00	0.00
Jania capillacea	0.00	0.00	0.00	0.00	0.00	0.00
Laurencia obtusa	0.00	0.00	0.00	0.00	0.00	0.00

Table 4 Continued

	MTC			LTC		
Diet Item	**% F**	**% Vind**	**% IRI**	**% F**	**% Vind**	**% IRI**
Lomentaria baileyana	0.00	0.00	0.00	0.00	0.00	0.00
Polysiphonia denudata	0.00	0.00	0.00	0.00	0.00	0.00
Pterocladiella bartlettii	0.00	0.00	0.00	0.00	0.00	0.00
Rhodymenia psuedopalmata	0.00	0.00	0.00	0.00	0.00	0.00
Spyridia filamentosa	0.00	0.00	0.00	0.00	0.00	0.00
Phaeophyta	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
Sargassum natans	0.00	0.00	0.00	0.00	0.00	0.00
Sargassum fluitans	0.00	0.00	0.00	0.00	0.00	0.00
Hincksia mitchelliae	0.00	0.00	0.00	0.00	0.00	0.00
Padina gymnospora	0.00	0.00	0.00	0.00	0.00	0.00
Rosenvingea orientalis	0.00	0.00	0.00	0.00	0.00	0.00
Dictyota menstrualis	0.00	0.00	0.00	0.00	0.00	0.00
Animal Matter	**33.33**	**99.88**	**33.29**	**25.00**	**19.01**	**4.75**
Phylum Porifera	0.00	0.00	0.00	25.00	19.01	4.75
Class Scyphozoa	0.00	0.00	0.00	0.00	0.00	0.00
Diopatra cupera	0.00	0.00	0.00	0.00	0.00	0.00
Family Penaeidae	33.33	18.65	6.22	0.00	0.00	0.00
Infraorder Brachyura	0.00	0.00	0.00	0.00	0.00	0.00
Class Bivalvia	0.00	0.00	0.00	0.00	0.00	0.00
Class Gastropoda	0.00	0.00	0.00	0.00	0.00	0.00
Class Ophiuroidea	0.00	0.00	0.00	0.00	0.00	0.00
Infraclass Teleostei	33.33	81.23	27.08	0.00	0.00	0.00
Other	**66.67**	**15.50**	**5.43**	**0.00**	**0.00**	**0.00**
Anthropogenic Debris	66.67	0.80	0.53	0.00	0.00	0.00
Terrestrial Plant Matter	33.33	14.71	4.90	0.00	0.00	0.00

Table 5. Percent occurrence (% F), percent volume by individual (% Vind) and percent index of relative importance (% IRI) of prey items in stomachs of >55 cm SCL green sea turtles stranding along the middle (MTC) and lower Texas coast (LTC) during 2007-2010. % Vind is the total volume for each diet item consumed by all turtles in the region.

	MTC			LTC		
Diet Item	**% F**	**% Vind**	**% IRI**	**% F**	**% Vind**	**% IRI**
Anthophyta	**100.00**	**90.63**	**94.74**	**100.00**	**111.05**	**92.26**
Halodule wrightii	100.00	90.47	94.69	44.44	24.37	10.83
Halophila decipens	33.33	0.16	0.05	11.11	1.83	0.20
Halophila engelmannii	0.00	0.00	0.00	11.11	0.52	0.06
Syringodium filiforme	0.00	0.00	0.00	88.89	28.49	25.32
Thalassia testudinum	0.00	0.00	0.00	100.00	55.84	55.84
Chlorophyta	**33.33**	**0.16**	**0.05**	**11.11**	**0.19**	**0.02**
Caulerpa mexicana	0.00	0.00	0.00	11.11	0.19	0.02
Chaetomorpha gracilis	0.00	0.00	0.00	0.00	0.00	0.00
Cladophora albida	0.00	0.00	0.00	0.00	0.00	0.00
Codium taylorii	0.00	0.00	0.00	0.00	0.00	0.00
Halimeda incrassata	0.00	0.00	0.00	0.00	0.00	0.00
Ulva fasciata	0.00	0.00	0.00	0.00	0.00	0.00
Ulva lactuca	33.33	0.16	0.05	0.00	0.00	0.00
Rhodophyta	**33.33**	**12.76**	**4.45**	**33.33**	**14.94**	**3.36**
Aglaothamnion halliae	0.00	0.00	0.00	0.00	0.00	0.00
Centrocerus clavulatum	0.00	0.00	0.00	0.00	0.00	0.00
Ceramium subtile	0.00	0.00	0.00	0.00	0.00	0.00
Digenea simplex	0.00	0.00	0.00	11.11	1.83	0.20
Gelidium crinale	0.00	0.00	0.00	0.00	0.00	0.00
Gracilaria cervicornis	0.00	0.00	0.00	0.00	0.00	0.00
Gracilaria tikvahiae	0.00	0.00	0.00	0.00	0.00	0.00
Grateloupia filicina	0.00	0.00	0.00	0.00	0.00	0.00
Halymenia floridana	0.00	0.00	0.00	0.00	0.00	0.00
Hydropuntia caudata	33.33	12.53	4.37	33.33	7.63	2.54
Hypnea musciformis	0.00	0.00	0.00	0.00	0.00	0.00
Hypnea spinella	0.00	0.00	0.00	0.00	0.00	0.00
Jania capillacea	0.00	0.00	0.00	11.11	3.66	0.41
Laurencia obtusa	0.00	0.00	0.00	11.11	1.83	0.20

Table 5 Continued

	MTC			LTC		
Diet Item	**% F**	**% Vind**	**% IRI**	**% F**	**% Vind**	**% IRI**
Lomentaria baileyana	33.33	0.23	0.08	0.00	0.00	0.00
Polysiphonia denudata	0.00	0.00	0.00	0.00	0.00	0.00
Pterocladiella bartlettii	0.00	0.00	0.00	0.00	0.00	0.00
Rhodymenia psuedopalmata	0.00	0.00	0.00	0.00	0.00	0.00
Spyridia filamentosa	0.00	0.00	0.00	0.00	0.00	0.00
Phaeophyta	**33.33**	**7.04**	**0.13**	**0.00**	**0.00**	**0.00**
Dictyota menstrualis	0.00	0.00	0.00	0.00	0.00	0.00
Hincksia mitchelliae	0.00	0.00	0.00	0.00	0.00	0.00
Padina gymnospora	0.00	0.00	0.00	0.00	0.00	0.00
Rosenvingea orientalis	0.00	0.00	0.00	0.00	0.00	0.00
Sargassum fluitans	0.00	0.00	0.00	0.00	0.00	0.00
Sargassum natans	33.33	7.04	0.13	0.00	0.00	0.00
Animal Matter	**33.33**	**1.41**	**0.49**	**55.56**	**30.60**	**4.36**
Phylum Porifera	0.00	0.00	0.00	44.44	29.32	4.22
Class Scyphozoa	0.00	0.00	0.00	0.00	0.00	0.00
Diopatra cupera	0.00	0.00	0.00	0.00	0.00	0.00
Family Penaeidae	0.00	0.00	0.00	0.00	0.00	0.00
Infraorder Brachyura	0.00	0.00	0.00	0.00	0.00	0.00
Class Bivalvia	0.00	0.00	0.00	0.00	0.00	0.00
Class Gastropoda	33.33	1.41	0.49	11.11	1.28	0.14
Class Ophiuroidea	0.00	0.00	0.00	0.00	0.00	0.00
Infraclass Teleostei	0.00	0.00	0.00	0.00	0.00	0.00
Other	**0.00**	**7.05**	**0.13**	**0.00**	**0.00**	**0.00**
Anthropogenic Debris	0.00	0.00	0.00	0.00	0.00	0.00
Terrestrial Plant Matter	33.33	7.05	0.13	0.00	0.00	0.00

turtles revealed patterns of prey consumption related to carapace length (Fig. 5). Other items consumed were terrestrial plant matter and anthropogenic debris (F <25%) not included in statistical analysis but presented in % IRI histogram. The most important dietary algal component for size classes >25 cm SCL in both regions was Rhodophyta. A major shift in diet importance from algae to seagrass with increasing turtle size regardless of sampling region was revealed. Anthophyta dominated the diet of LTC turtles >25 cm SCL (F ≥64%) and MTC turtles >35 cm SCL (F ≥66.7%). Animal matter consumption was recorded across all size ranges in both regions. Anthropogenic debris was consumed by turtles <55 cm SCL (F = 20.17%); the individual volume range was 0.1 to 37.5 ml.

Regional Diet Comparison. The comparative histogram of the principal diet items (F ≥25%) ingested between each 10-cm SCL size range created for both regions revealed a size-based trend. Juvenile green turtles consumed a variety of items that differed between the regions for similar size classes (Table 1-5). Rhodophyta was consumed differentially among the five size classes of MTC turtles (Welch ANOVA $F_{4,8.565} = 3.98$, $p < 0.05$). Post hoc comparison using the Games-Howell test denoted that ingestion of Rhodophyta algae was significantly different between 25-34.9 cm SCL (M = 0.313, SD = 0.322) and >55 cm SCL turtles (M = 0.039, SD = 0.068). The ingestion of Rhodophyta by 25-34.9 cm SCL turtles along the MTC (M = 0.313, SE = 0.049) and LTC (M = 0.169, SE = 0.045) also differed significantly $t(63.41) = 2.151$, $p < 0.05$.

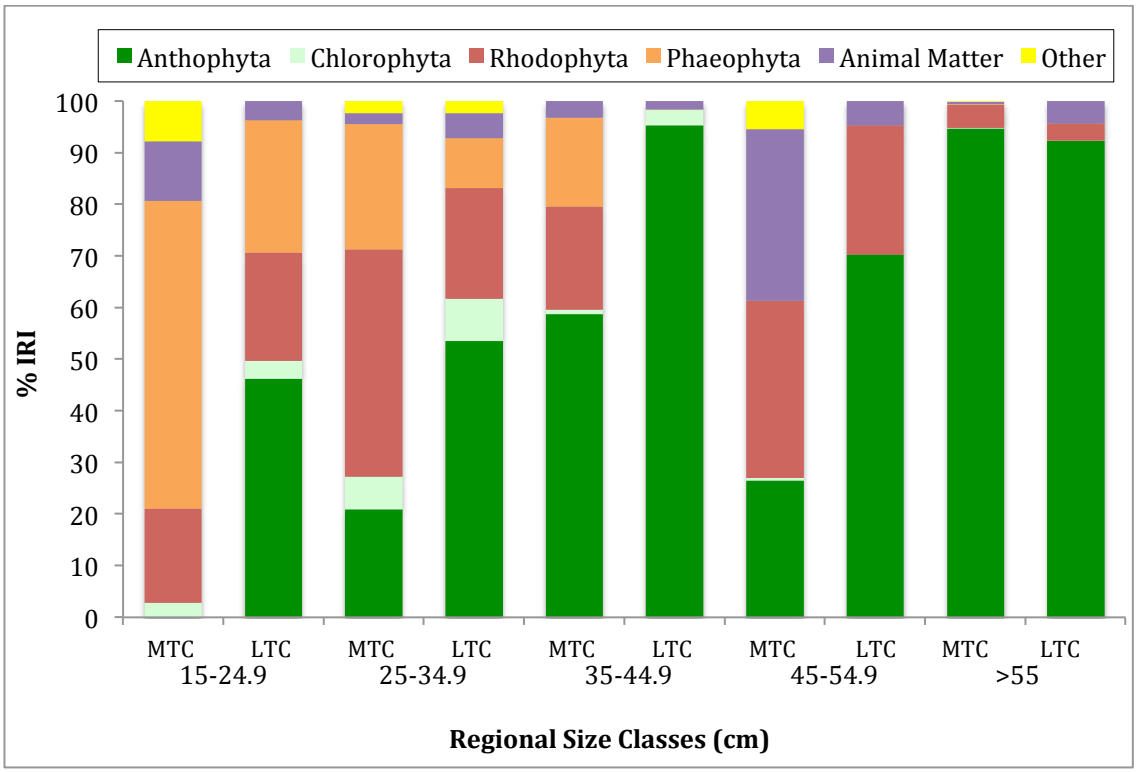


Figure 5. Percentage IRI of principal diet items consumed by each size class of juvenile green sea turtles stranding along the middle and lower Texas coast during 2007-2010.

Consumption of Anthophyta differed significantly among the five size classes foraging along the MTC ($F_{4,58}$ = 5.007, p <0.05). Anthophyta intake for turtles >55 cm SCL differed significantly from that of 15-24.9 and 25-34.9 cm SCL turtles (Games Howell test). Anthophyta ingestion among the five size classes from the LTC differed significantly (Welch ANOVA $F_{4,11.609}$ = 5.344, p <0.05). Games Howell post hoc comparison revealed a significant difference in Anthophyta consumption between 25-34.9 cm SCL greens (M = 0.376 SD = 0.336) and their 35-44.9 (M = 0.671 SD = 0.046) and >55 cm SCL conspecifics (M = 0.655 SD = 0.049). Anthophyta ingestion of 25-34.9 cm SCL turtles differed significantly between the MTC (M = 0.153, SE = 0.039) and LTC (M = 0.376, SE = 0.067) $t(40.63) = -2.857$, p <0.05. No other significant differences in forage material intake were detected between the regions (p >0.05).

DISCUSSION

Diet Description. Diet analysis revealed that Texas' juvenile green turtles are predominantly herbivorous, with the primary taxon of forage strongly associated with turtle size. Coyne (1994) indicated juvenile green turtles exhibit diet selectivity in south Texas. A single alga or seagrass species made up more than 50% of the foregut volume in 87% of the samples in this study. Monotypic diet selection suggests that turtles were targeting a specific item, though diet selection is ultimately determined by the presence of preferred items (Garnett et al. 1985).

Many species use similar resources when small, but diverge in niche

when older so as to maximize absolute growth rates and energy at each size (Jud et al. 2011). Rapid growth of the juvenile phase of many organisms, including sea turtles (Bjorndal et al. 2000), is accompanied by an ontogenetic habitat shift as a means of increasing or maintaining growth rate (Werner & Gilliam 1984). The shift from oceanic to nearshore habitat was evident within the diet of turtles ≤20 cm SCL that ingested primarily *Sargassum* spp., *Schyphozoa* spp. and anthropogenic debris, previously reported as oceanic stage diet items (Plotkin & Amos 1990, Boyle & Limpus 2008, Parker et al. 2011). The smallest green turtles recruiting into nearshore areas typically use structured environments for protection and predator avoidance (Musick & Limpus 1997). It is here that jetties function as an intermediate developmental habitat between the oceanic environment and lagoonal feeding pastures (Shaver 2000). Larger turtles, 20 to 24.9 cm SCL, consumed benthic neritic diet items and, consequently, were presumed to be residing along nearshore territory. Reptile bite size has been reported to facilitate nutrient assimilation (Bjorndal 1997) by allowing ingestion of smaller food particles that are more rapidly fermented (Bjorndal et al. 1990). Comparatively, algae diet samples were more heavily fragmented than were seagrasses, suggesting turtles foraging at jetty habitat are potentially obtaining nourishment that results in overall faster growth (Shaver 1994). Green turtles are vulnerable to exploitation because of their slow growth and delayed maturity as a result of their herbivorous diet (Bjorndal 1985); consequently, it would be highly advantageous to maximize nutritional gain and

subsequent growth while in the jetty habitat. Ultimately, in order to define diet quality and nutrition gained, measurements of intake and digestibility need to be determined (Bjorndal 1980). Ingestion of Rhodophyta algae occurred within every size class, and it was the dominant algal taxon consumed for >25 cm SCL turtles. The most frequently ingested Rhodophyta algae, *Hydropuntia caudata,* in turtles >45 cm SCL was intermixed with large amounts of seagrass, suggesting this algal sp. is present within the seagrass beds.

Additional dietary and habitat shifts within neritic foraging grounds have been described, wherein smaller age classes of green turtles consumed macroalgae and mangrove taxa while larger age classes ingested primarily seagrasses (Arthur et al. 2008). Tracking data revealed that turtles occupying jetty environment make brief excursions into the bay but return to the jetty environment (Shaver 2000). By contrast, turtles that recruit to the seagrass beds tend to persist within it and rarely move northward within the Laguna Madre (Shaver 2000). Digestive efficiency is increased by digestive alteration, aiding foragers to meet metabolic demands despite a shifting resource base (Whelan et al. 2000). Size-based habitat segregation of green turtles within Texas' neritic benthic zone is most evident with the observed diet change from benthic algae to seagrasses in 25-44.9 cm SCL turtles. Seagrass consumption correlated with increasing size of turtles: 53% in size range 25-34.9 cm SCL and 100% in >55 cm SCL turtles. Seemingly, the jetty region lacks sufficient resources to support nutritional needs of >35 cm SCL turtles, with this constraint driving the larger

juveniles from the jetties and into seagrass beds where they forage on abundant, nutrient-rich food resources that facilitate further growth. *T. testudinum* has been acknowledged as a major diet item for green turtles in the Caribbean (Bjorndal 1980, Mortimer 1981). It was found to be a principal dietary item in >60% of turtles >25 cm SCL in this study. The expansion of *T. testudinum* beds (Onuf 1996, Kaldy & Dunton 1999, Onuf 2007) within Texas bay systems may contribute to the dominance of this seagrass sp. in the diet as well as the distribution and abundance of green turtles.

Invertebrate ingestion has also been documented in green turtles (Seminoff et al. 2002, López-Mendilaharsu et al. 2005). Animal matter supplemented the diet of all size classes of juvenile green sea turtles examined in this study. Incidental consumption of animal matter by green turtles has been suggested (Guebert-Bartholo et al. 2011).

Stranded turtles along the Texas coast have previously been noted to forage on anthropogenic debris (Plotkin & Amos 1988, Shaver 1991, 2000). Consumption of even small quantities of debris can have severe health consequences including mortality in sea turtles (Bjorndal et al. 1994). Ingestion of marine debris was evident in 20% of stomachs analyzed in the present study, with several additional turtles from each size class observed to have debris in their intestines, which were not included in analysis. The majority of turtles that had consumed debris were presumed to be occupying oceanic and jetty habitat based on other diet items consumed. Presence of debris in juvenile green turtles

is alarming, especially given the rapid increase in plastic debris in the marine environment (Moore 2008). As a recovery-task priority item for the green sea turtle, this striking consumption of anthropogenic debris needs to be addressed by conservationists and managers assigned to the recovery of this species.

***Regional Diet Comparison*.** Juvenile green turtle feeding ecology differed significantly between the two regions of the Texas coast from which samples were collected. Marine vegetation assemblages in the green turtle diet were dissimilar among the two study areas, a finding consistent with results from analogous studies (Forbes 1996). Reported disparities in macroalgae and seagrass availability, as well as flora abundance along the Texas coast (Conover 1964, Pulich & Onuf 2007), could explain the observed diet differentiations between the two regions. Size ranges of green turtles consuming neritic benthic algae and seagrasses differed between the two regions. Specifically, turtles 25 to 34.9 cm SCL within the two regions consumed Rhodophyta and Anthophyta disproportionally. High % IRI ranking of Anthophyta in 25-34.9 cm SCL turtles from the LTC suggests the transition to bay systems occurs at a smaller size than does that for MTC counterparts that exhibited a high Rhodophyta % IRI ranking. Not until MTC turtles reach 35-44.9 cm SCL do % IRI values indicate that Anthophyta has become the most important dietary resource in this region. Differences in habitat type and food availability have resulted in significant growth rate variations for juvenile green turtles among the diverse regions of the Florida Atlantic coast (Kubis et al. 2009). Rapidly growing

individuals shift niches at a smaller size and are energetically constrained by limited food resources due to their higher metabolic rates (Guebert-Bartholo et al. 2011). Nutritional differences due to forage material may be one of the influential factors for the regional size discrepancies demonstrated among the jetty environment of the Texas coast. Also, as metabolic rate is closely coupled to water temperature in ectotherms, regional water temperature differences may also drive the reported dissimilarities in green sea turtle size ranges occupying the two habitats. Fast growing young turtles along the warmer LTC might not utilize the jetty region for as long of a time period, thus transitioning to the seagrass beds earlier than do most MTC turtles.

Continuing expansion of seagrasses along the LTC (Onuf 2007) provides green turtles with more extensive areas over which to forage. Seagrass beds within the MTC is not as vast as that in the LTC, a difference that may result in MTC green turtles occupying resource-abundant jetties longer prior to transitioning to bay systems. With the recent enactment of the seagrass protection measures along an area of the MTC (TPWD 2012), an increase in seagrass abundance should occur. Conceivably, MTC turtles could start to exhibit a similar tendency to that of 25-34.9 cm SCL LTC turtles, recruiting to seagrass beds at a smaller size class.

It was anticipated that seagrass consumption would only occur in turtles >30 cm SCL (Coyne 1994); however, a few 15-24.9 cm SCL LTC turtles had ingested significant amounts of seagrasses, resulting in a high Anthophyta % IRI

ranking for this size class. Noteworthy, is that observed seagrass in turtle stomachs was in relatively healthy condition, not at all similar to the deteriorated condition of grass blades observed floating at the surface (L.N.H person. observ.).

The principal animal in the diet of LTC turtles >45 cm SCL was sponges. Ingestion of sponges has been observed in *C. mydas* (Mortimer 1981), with deliberate consumption proposed (Russell et al. 2011). Bjorndal et al. (1990) documented green turtles consuming sponges with *T. testudinum* and suggested its importance in the diet as providing a trace mineral, vitamin, or essential amino acid. Sponges may provide nutritional benefits while meeting necessary diet requirements of these seagrass bed recruits.

In contrast to the seagrass dominated diet of LTC 45-54.9 cm SCL turtles, the most important diet items for this size range of MTC turtles were Rhodophyta and animal matter. Two of the three turtles consumed the red alga, *H. caudata,* in conjunction with seagrasses, while the third turtle consumed only animal matter. Individual specialization in foraging habits of same size class turtles has been recently illustrated (Vander Zanden et al. 2010, Burkholder et al. 2011). As such, the aforementioned individual may represent a group of 45-54.9 cm SCL turtles within the MTC that selectively target animal matter due to limiting resources. However, results must be interpreted with caution due to the limited sample size (n=3) for 45-54.9 cm SCL turtles from the MTC. Further analysis of turtles in this size class is necessary to determine any patterns of specialization

within jetty and seagrass habitats. Regardless of sampling region, diet analysis illustrated multiple shifts in habitat and diet occur with increasing turtle size.

CHAPTER III

DIET AND HABITAT SHIFTS OF GREEN SEA TURTLES INVESTIGATED THROUGH STABLE ISOTOPE ANALYSIS OF ^{13}C AND ^{15}N

INTRODUCTION

Stable isotope analysis is a valuable technique in ecology for determining trophic status, food web dynamics, and migration patterns (DeNiro & Epstein 1978, 1981, Hobson et al. 1997, Layman et al. 2005, Fry 2006, Hoeinghaus & Zeug 2008). It has been used to elucidate sea turtle foraging dynamics as well as migration patterns and resident habitat choices (Godley et al. 1998, Hatase et al. 2002, Reich et al. 2007, Reich et al. 2010, Vander Zanden et al. 2010, Pajuelo et al. 2012). Dietary inferences can be drawn from the isotope ratio of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ retained in the tissues of a consumer because stable isotopes in the tissue of organisms reflect their assimilated diet in a predictable pattern (DeNiro & Epstein 1978, 1981). Marine ecosystems exhibit several isotopic gradients; depleted $\delta^{13}C$ in the oceanic and pelagic realm and at higher latitudes, and enriched $\delta^{13}C$ in benthic and neritic zones and at low latitudes (Fry et al. 1977, France 1995, Michener 2007). Consumers within a food web that are dependent on producers enriched in $\delta^{13}C$ will maintain those enriched values throughout the trophic network (Smit 2005). There is also a consistent enrichment of $\delta^{15}N$ with trophic level. Consequently, it is possible to determine trophic positions of organisms within the same food web (Hobson et al. 2000).

Changes in isotope ratios from the environment to the consumer's tissue, termed isotope discrimination (DeNiro & Epstein 1978, 1981), are likely influenced by multiple factors. Some of these factors include species, tissue type (Hobson & Clark 1992), growth (Reich et al. 2008), metabolic fractionation (Fry 2006), protein quality and quantity (Tsahar et al. 2008), and nitrogen waste excretion (Vanderklift & Ponsard 2003). Diet tissue discrimination factors have been determined for several sea turtle species (Seminoff et al. 2006, Reich et al. 2008, Seminoff et al. 2009) and subsequently these values are applied to the isotope values of potential forage material to provide inferences in trophic status and habitat occupation (Revelles et al. 2007, Wallace et al. 2009, McClellan et al. 2010, Dodge et al. 2011). It is essential to recognize both isotope discrimination and turnover rate (the period of time the isotope is retained in the tissue of the consumer) in order to accurately interpret isotope results from the tissue sampled. More metabolically active tissues (i.e. plasma solutes, liver) have faster turnover rates than do less active tissues (i.e. epidermis, bone) (Hobson & Clark 1992, Bosley et al. 2002, Reich et al. 2008, Alves-Stanley & Worthy 2009). Tissues, such as otoliths and baleen, that remain inert after synthesis, maintain a history of an organism's habitat and diet at the time of tissue formation (Hobson 1999). Sea turtle scute, comprised of metabolically inert and continuously growing keratin, retains the isotopic composition of resources incorporated at the time of tissue synthesis. Stable isotope analysis of sequential layers of scute yields a chronological profile of isotope values that

can be used to identify the time-integrated diet and habitat shifts for a given turtle (Reich et al. 2007). These factors collectively demonstrate that scute is an advantageous tissue for determining changes in diet and habitat over time.

Stable isotope analysis is most valuable when providing information on changes in diet and habitat use of two isotopically distinct dietary sources (Hobson & Clark 1992). Analysis of $\delta^{13}C$ and $\delta^{15}N$ values in oceanic-stage green turtles in the Pacific illustrated that they forage at a higher trophic level than do recruits to seagrass beds (Arthur et al. 2008). Gorga (2010) applied stable isotope analysis of scute from live entanglement-netted and rehabilitated green turtles to determine a 2 to 3 year residency on Texas' algae-laden jetties. Isotope values also revealed that, at 35 - 45 cm SCL, these individuals moved from jetty channels into bay systems with a subsequent diet shift from algae to seagrasses.

Investigating isotope values in metabolically inert tissue of several size ranges is necessary to thoroughly document the multiple shifts that juvenile green turtles may exhibit along the Texas coast. The working hypothesis is that turtles < 25 cm SCL will exhibit tissues enriched in $\delta^{15}N$ and depleted in $\delta^{13}C$, indicative of an omnivorous oceanic stage. New recruits to the neritic zone, 25 to 34.9 cm SCL, will have new tissues enriched in $\delta^{13}C$ and slightly depleted in $\delta^{15}N$ values revealing foraging on macroalgae in jetty environment. It is assumed the oldest tissue will be indicative of the oceanic zone occupied and omnivorous diet consumed. Larger juveniles will exhibit new tissue isotope

values that are more enriched in $\delta^{13}C$ and depleted in $\delta^{15}N$, given their nutritional dependence on seagrasses (Coyne 1994), with the oldest tissues indicative of previous diets and habitats occupied.

MATERIALS AND METHODS

Stable Isotope Data Collection. Samples for stable isotope analysis were collected from all 114 stranded turtles utilized for stomach contents analysis (see Chapter II). Scute tissue of each stranded carcass was collected from the second costal scute of the carapace (Fig. 6) following protocol outlined in Reich et al. (2007). Areas sampled were cleaned to remove superficial epibiota and then cleansed with sterile alcohol. A sterile 6 mm biopsy punch was used to remove tissue from the anterior region of the scute; the sample was subsequently stored in 70% ethanol solution for future analysis. In preparation for stable isotope analysis, samples were removed from the ethanol, each sample surface was wiped additionally with sterile alcohol, rinsed with deionized water, and then placed in a drying oven at 60°C for 24 hours. Lipids were extracted from samples using a Dionex Accelerated Solvent Extractor 350, with petroleum ether as the solvent. The scute sample was adhered to a slide dorsal side down to allow the most recently synthesized tissue to be sampled. Each scute sample was microsectioned using a carbide end mill in successive 50-micron layers of oldest to newest synthesized tissue. The layers generated were individually weighed and loaded into a precleaned tin capsule for analysis

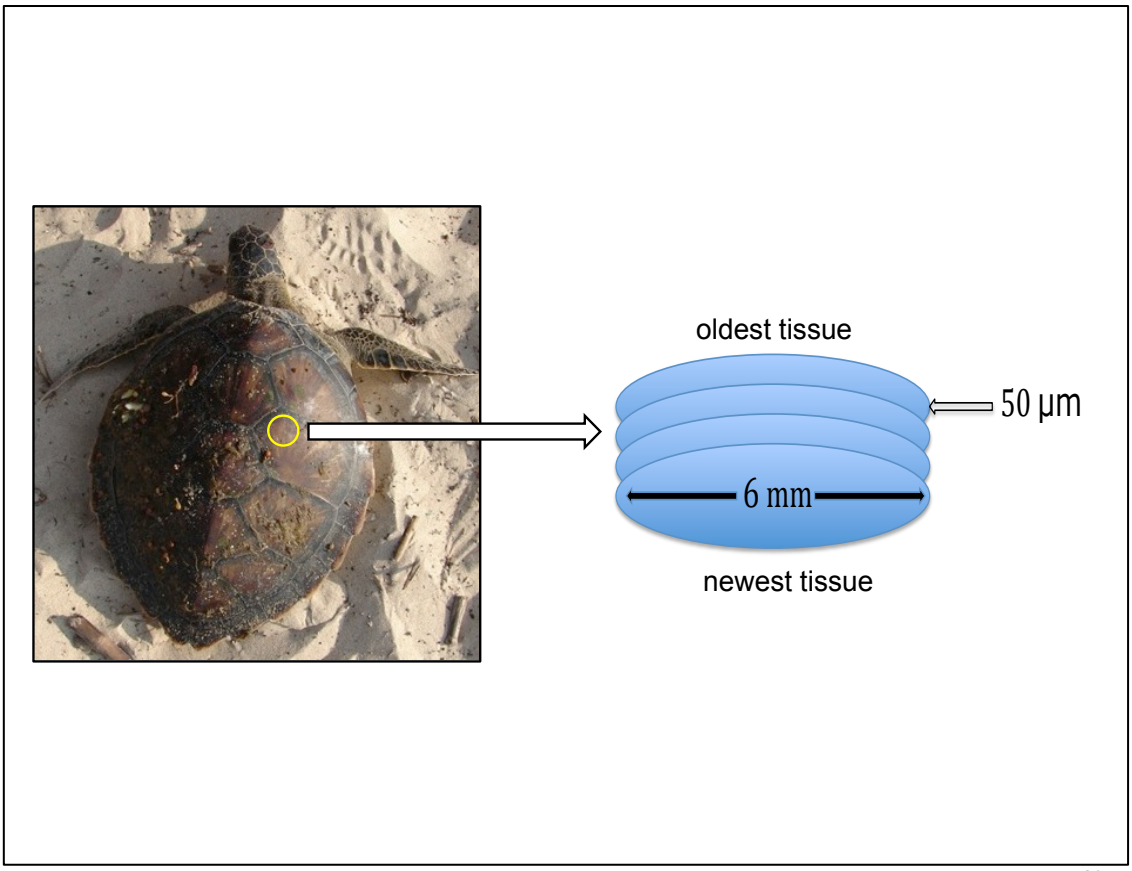


Figure 6. Scute biopsy sampling location for stable isotope analysis of ^{13}C and ^{15}N from juvenile green sea turtles stranding along the middle and lower Texas coast during 2007-2010.

of $\delta^{15}N$ and $\delta^{13}C$ and sent to the University of Florida's Stable Isotope Lab. Each sample was combusted using a COSTECH ECS 4010 elemental analyzer interfaced via a Finnigan-MAT Conflow III device to a Finnigan-MAT DeltaPlus XL isotope ratio mass spectrometer. Stable isotope values were expressed in standard delta (δ) notation, defined as parts per thousand (‰) relative to the standard as follows:

$$\delta^{H}X = (R_{SAMPLE}/R_{STANDARD} - 1) * 1000.$$

In this formula, the δ notation is for a particular element (X); the superscript H is the heavy isotope mass of that element; and R is the corresponding ratio of heavy to light isotopes ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) in the sample and international standard. The standard for ^{13}C is the Vienna Pee Dee Belemnite (VPDB) limestone formation. The standard for ^{15}N is atmospheric N_2.

Stable Isotope Data Analysis. Data were examined for 10-cm SCL size classes (see Chapter II). Statistical analyses were undertaken using IBM SPSS 19.0 statistical software. Data were tested for normality; Levene's test was used to test for homogeneity of variances, and Welch ANOVA was applied to account for unequal variances. Statistical analyses were applied to the newest tissue from each turtle. Isotope values of the same size classes for each region were compared with a Students t-test to demonstrate any regional differences. A one-way ANOVA was employed to compare $\delta^{13}C$ and $\delta^{15}N$ between life history stages. When ANOVA was significant, a multiple pairwise comparison test was utilized to explore between-group differences of isotope values. The overall

distribution of all size classes' newest tissue isotope values was examined for trends across size classes for each region. The successive layers of scute material analyzed for each individual generated stable carbon and nitrogen isotope profiles of oldest to newest tissue which allowed potential diet and habitat shifts to be examined.

RESULTS

Analysis of Stable Isotopes from Juvenile Green Turtles on the MTC. Isotope values of $\delta^{13}C$ in scute samples varied between members of each of the five size classes from the MTC. Values ranged from -19.52 to - 7.26‰. Mean $\delta^{13}C$ value for each size class (Fig. 7) was: 15-24.9 cm SCL: -17.66‰ ± 1.02, 25-34.9 cm SCL: -17.52‰ ± 1.77, 35-44.9 cm SCL: -14.09‰ ± 3.72, 45-54.9 cm SCL: -12.07‰ ± 3.49, and >55 cm SCL: -7.94‰ ± 1.11. Comparably, the $\delta^{15}N$ values of scute from all size classes ranged from 4.41 to 15.25‰. Mean $\delta^{15}N$ value (Fig. 7) for each size class was: 15-24.9 cm SCL: 9.86‰ ± 2.13, 25-34.9 cm SCL: 10.99‰ ± 1.76, 35-44.9 cm SCL: 10.53‰ ± 2.53, 45-54.9 cm SCL: 10.40‰ ± 2.86, and >55 cm SCL: 5.57‰ ± 1.01. MTC $\delta^{13}C$ values differed significantly among all size classes (Welch ANOVA $F_{4,4.851} = 13.793$, $p < 0.05$) as well as did counterpart $\delta^{15}N$ values for the five size classes (ANOVA $F_{4,58} = 5.811$, $p < 0.05$). Post hoc comparison using Gabriel analysis detected a significant difference between the $\delta^{13}C$ values of >55 cm SCL turtles and those of all other size classes ($p < 0.05$). Similarly, $\delta^{15}N$ values for >55 cm SCL turtles were significantly different from those of the other size ranges ($p < 0.05$).

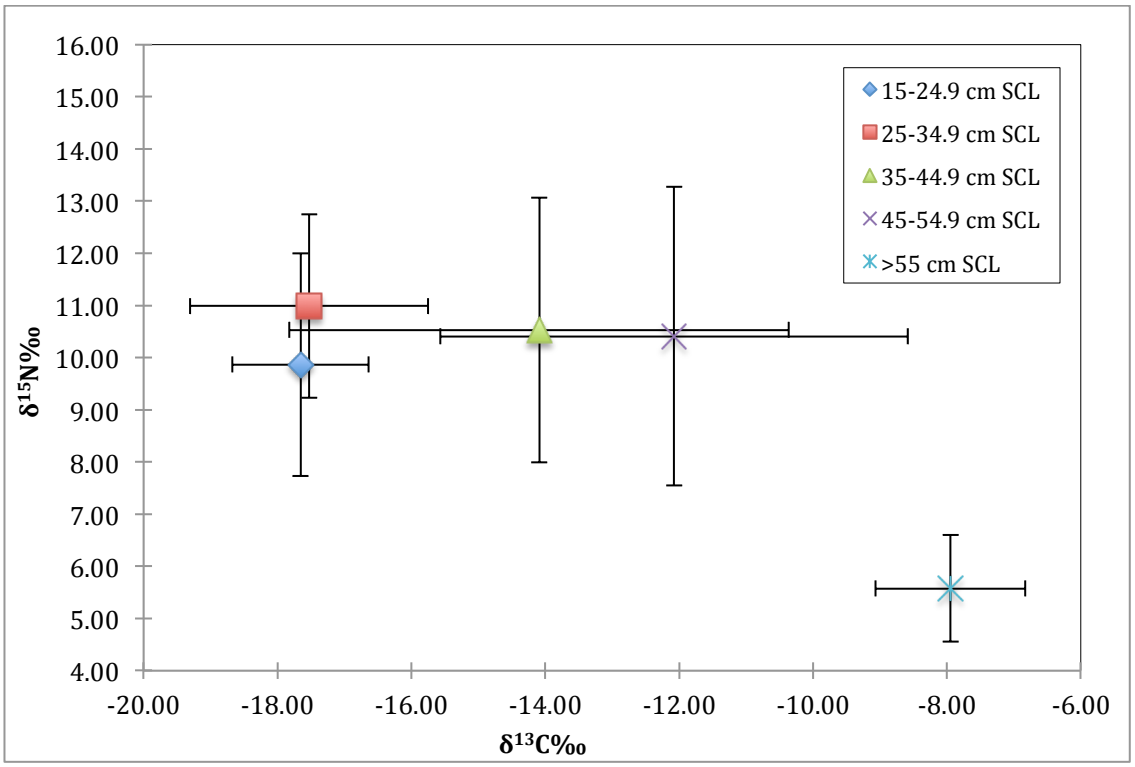


Figure 7. Mean $\delta^{13}C$ and $\delta^{15}N$ values (± SD) for the newest scute tissue of green sea turtles stranding along the middle Texas coast during 2007-2010.

Distributions of isotope values of the newest tissue from all individuals (Fig. 8a, b) depicted changes in isotope concentrations with increasing turtle size.

Isotope Profiles of Juvenile Green Turtles on the MTC. Individual isotope profiles (all layers from a single sample) for stable carbon and nitrogen for representatives of each size class revealed size based shifts in isotope concentrations. Enrichment of $\delta^{13}C$ values from the oldest to newest scute tissue of the 15-24.9 cm SCL size class was observed (Fig. 9a). The $\delta^{15}N$ values also showed enrichment across the tissue layers (Fig. 9b), with the oldest layer's values approximating most closely those of omnivorous greens (Cardona et al. 2009). $\delta^{13}C$ values for 25-34.9 cm SCL turtles (Fig. 10a) changed from oceanic isotope values in their oldest tissue to an enriched concentration of isotopes in the newest synthesized tissue. Similarly, the $\delta^{15}N$ values showed depletion across the tissue layers of most 25-34.9 cm SCL turtles (Fig. 10b). Several 35-44.9 cm SCL turtles exhibited a successive shift in isotope concentrations, with stepwise enrichment of $\delta^{13}C$ and depletion of $\delta^{15}N$ (Fig. 11a,b). All 45-54.9 cm SCL turtles demonstrated almost identical changes in $\delta^{13}C$ and $\delta^{15}N$ values (Fig. 12a,b). Isotope profiles for two >55 cm SCL turtles yielded depleted $\delta^{15}N$ values and enriched $\delta^{13}C$ values from oldest to newest tissue, while that for the remaining turtle varied little in $\delta^{13}C$ and $\delta^{15}N$ values (Fig. 13a,b).

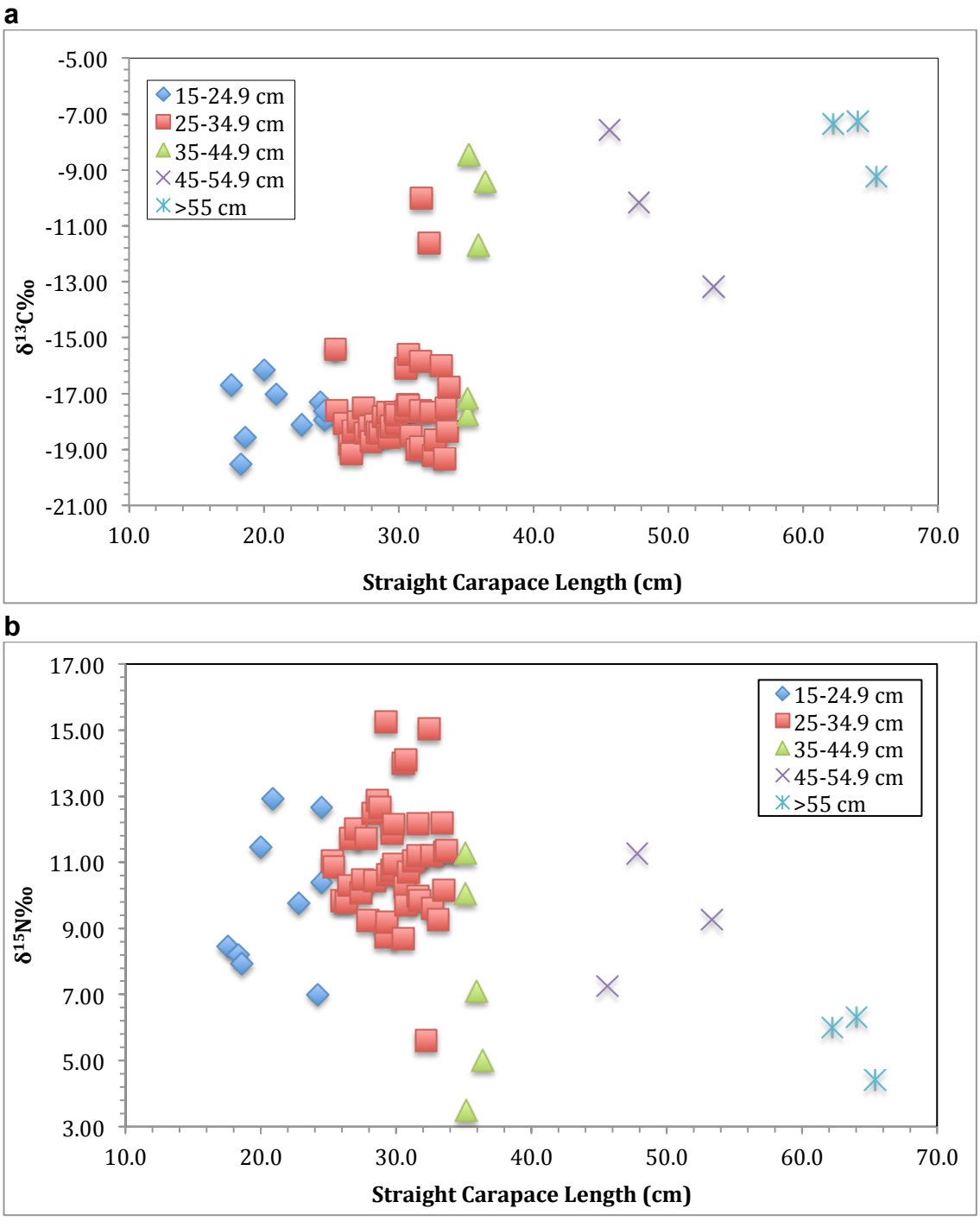
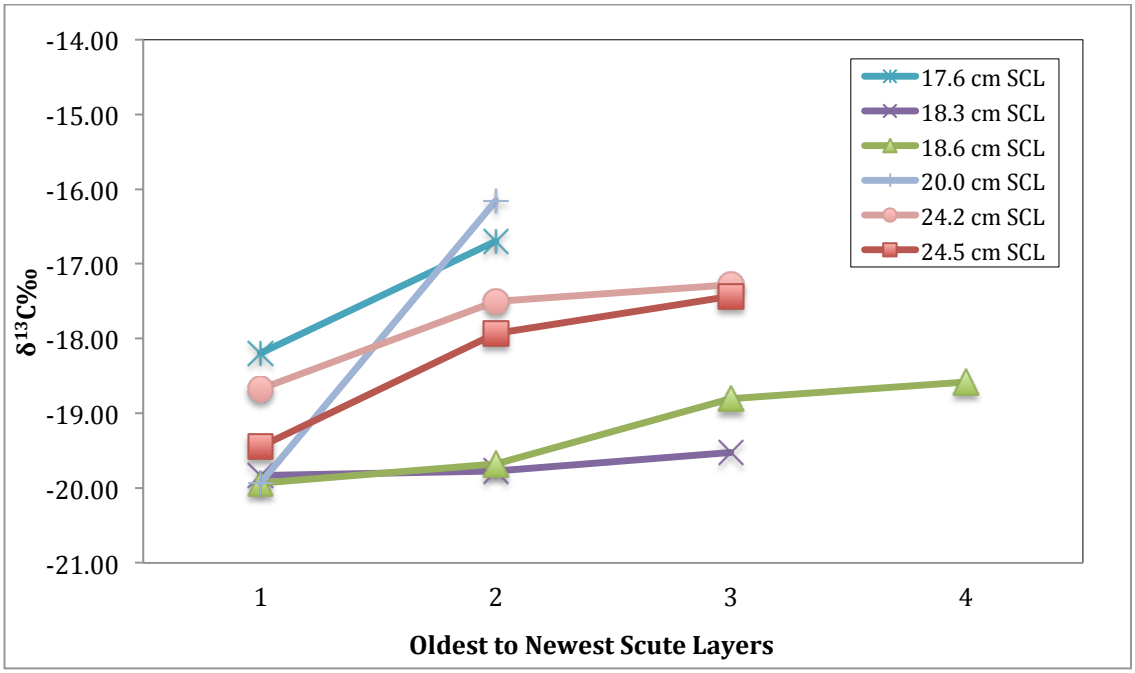


Figure 8. Distribution of (a) $\delta^{13}C$ values and (b) $\delta^{15}N$ values in newest scute tissue versus straight carapace length of green sea turtles stranding along the middle Texas coast during 2007-2010 (n = 63).

a



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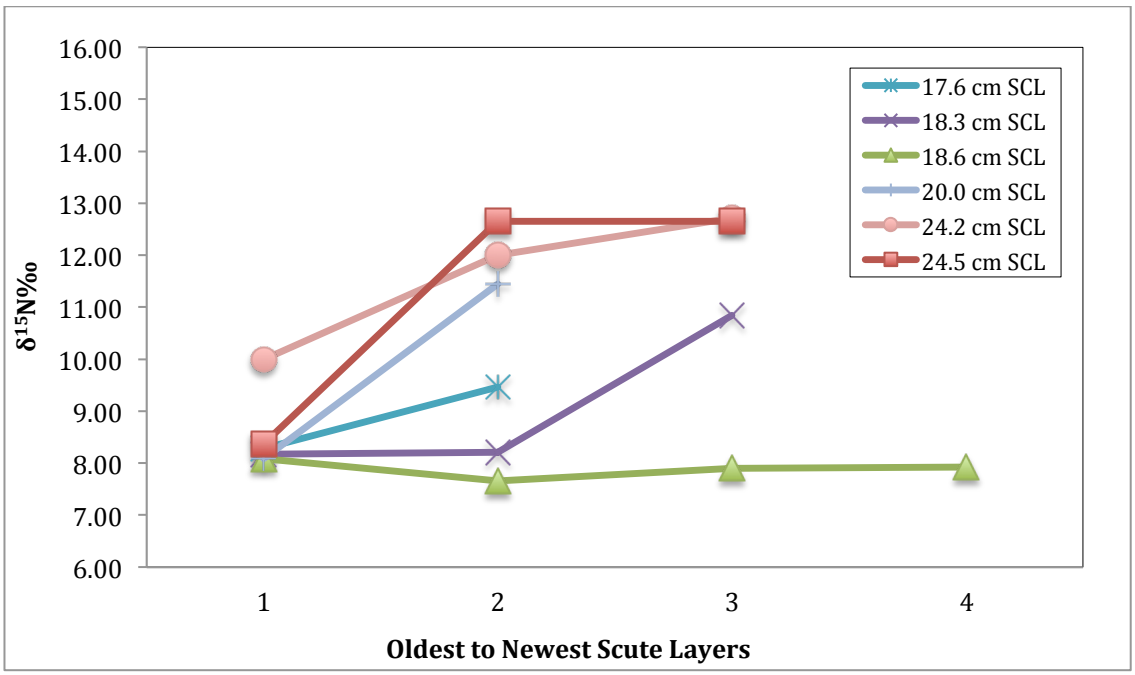
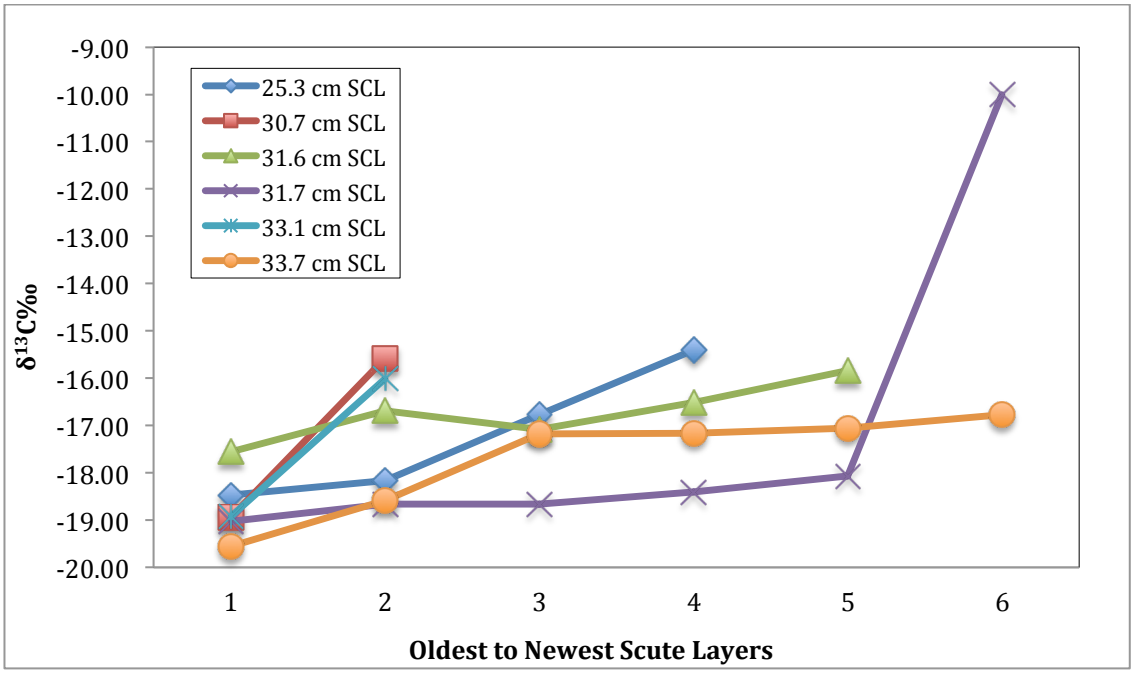


Figure 9. Isotope profiles of the (a) $\delta^{13}C$ values and (b) $\delta^{15}N$ values for scute tissue from the 15-24.9 cm SCL green sea turtle size class stranding along the middle Texas coast during 2007-2010.

a



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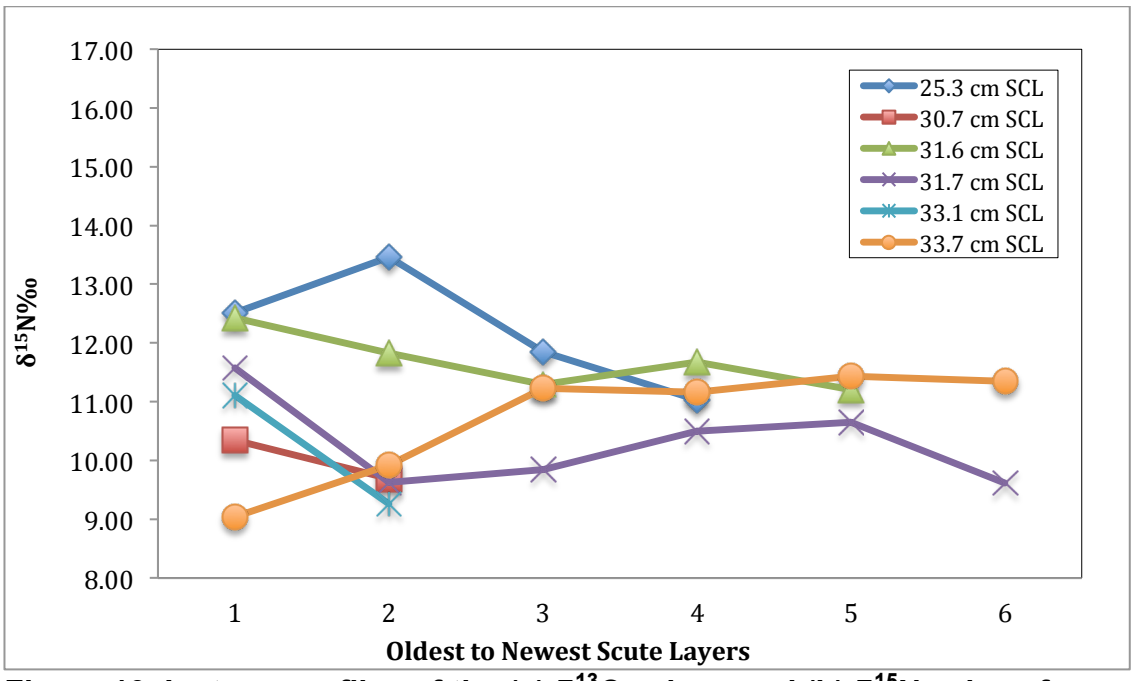
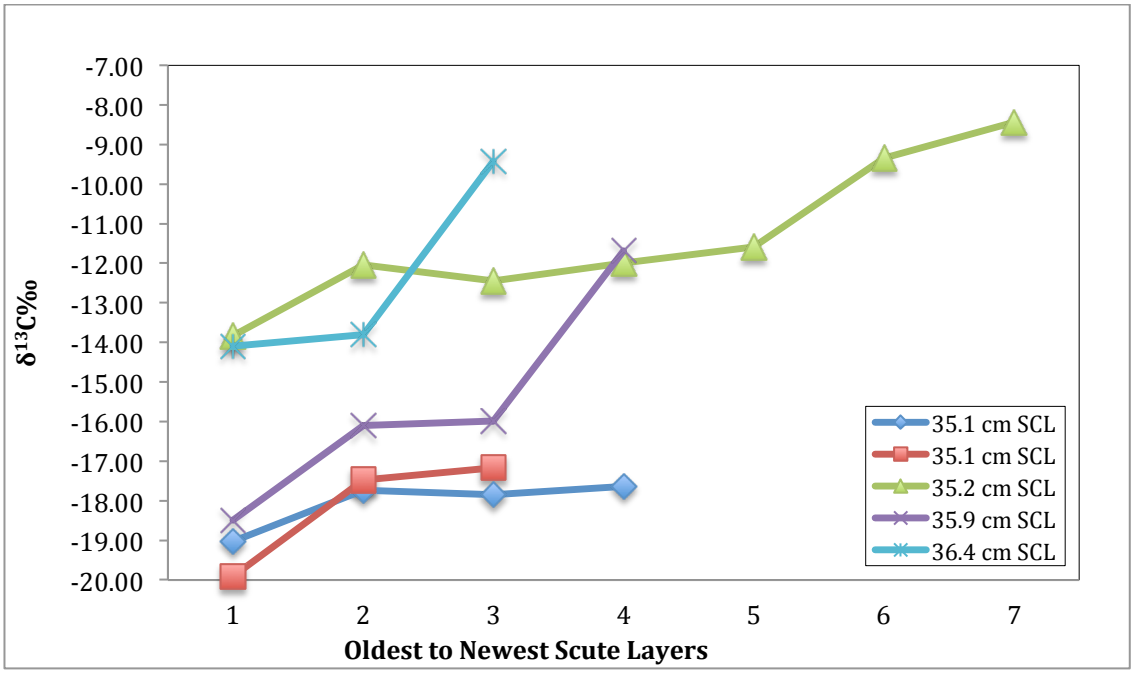


Figure 10. Isotope profiles of the (a) $\delta^{13}C$ values and (b) $\delta^{15}N$ values for scute tissue of the 25-34.9 cm SCL green sea turtle size class stranding along the middle Texas coast during 2007-2010.

a



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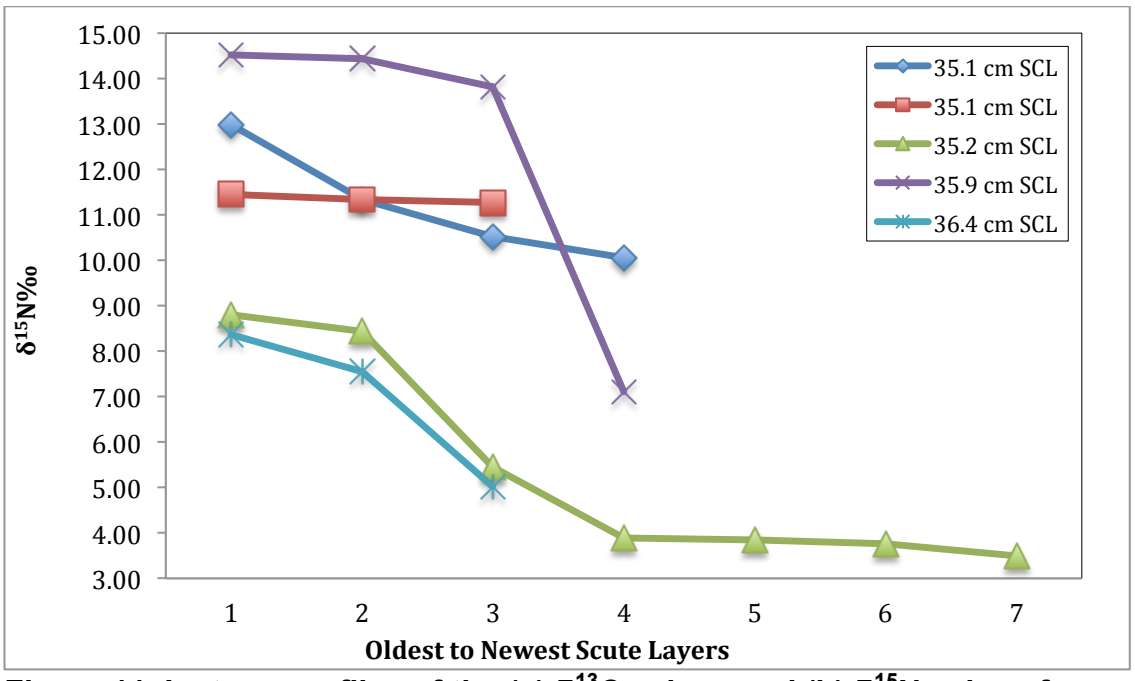
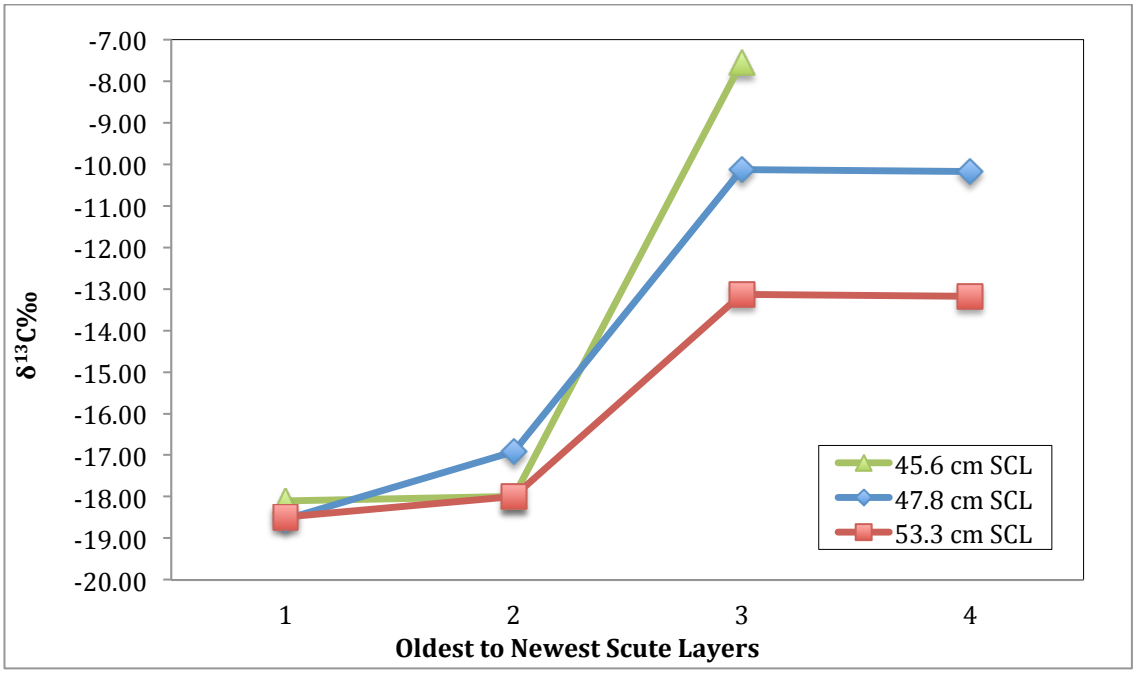


Figure 11. Isotope profiles of the (a) $\delta^{13}C$ values and (b) $\delta^{15}N$ values for scute tissue of the 35-44.9 cm SCL green sea turtle size class stranding along the middle Texas coast during 2007-2010.

a



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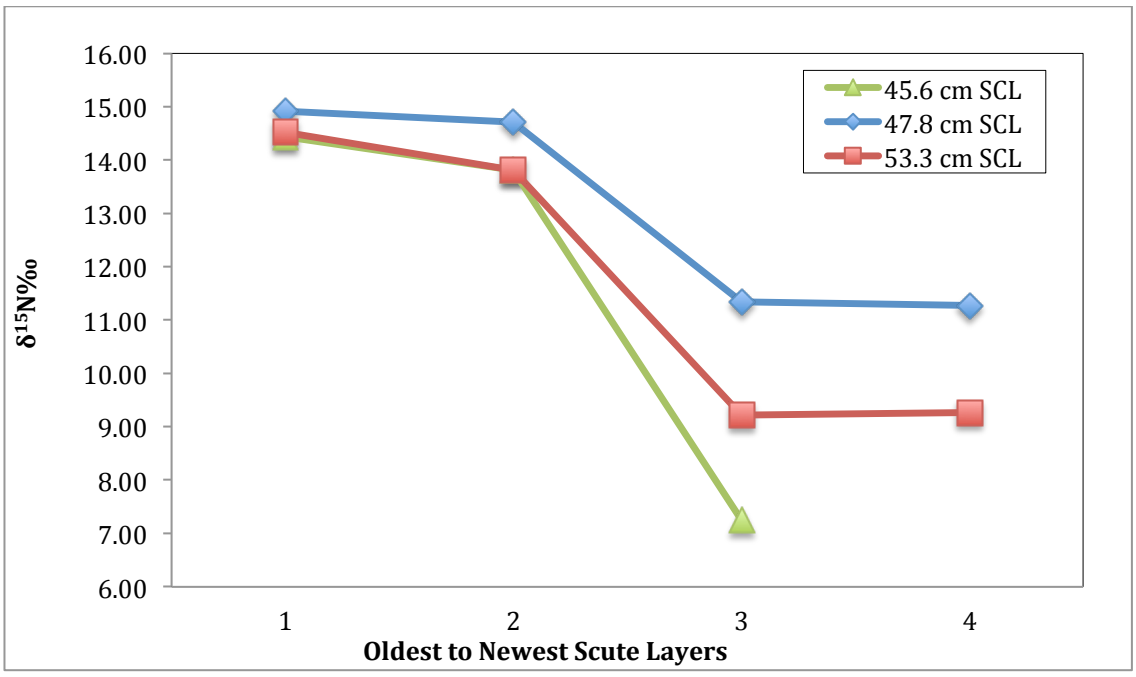
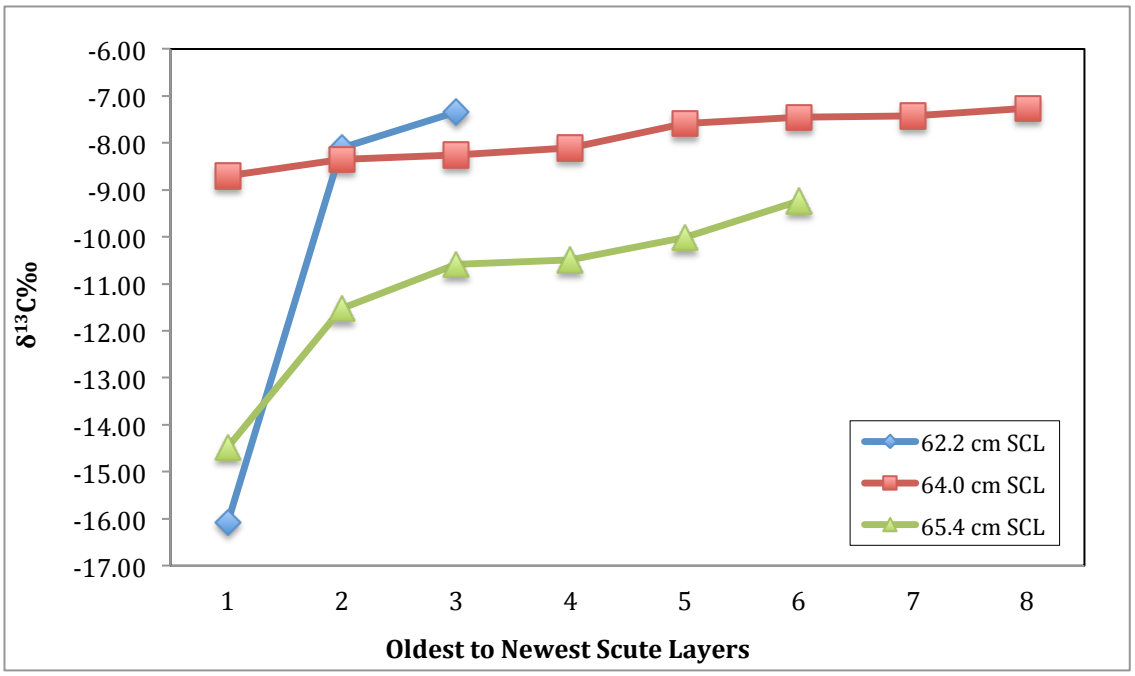


Figure 12. Isotope profiles of the (a) $\delta^{13}C$ values and (b) $\delta^{15}N$ values for scute tissue of the 45-54.9 cm SCL green sea turtle size class stranding along the middle Texas coast during 2007-2010.

a



b

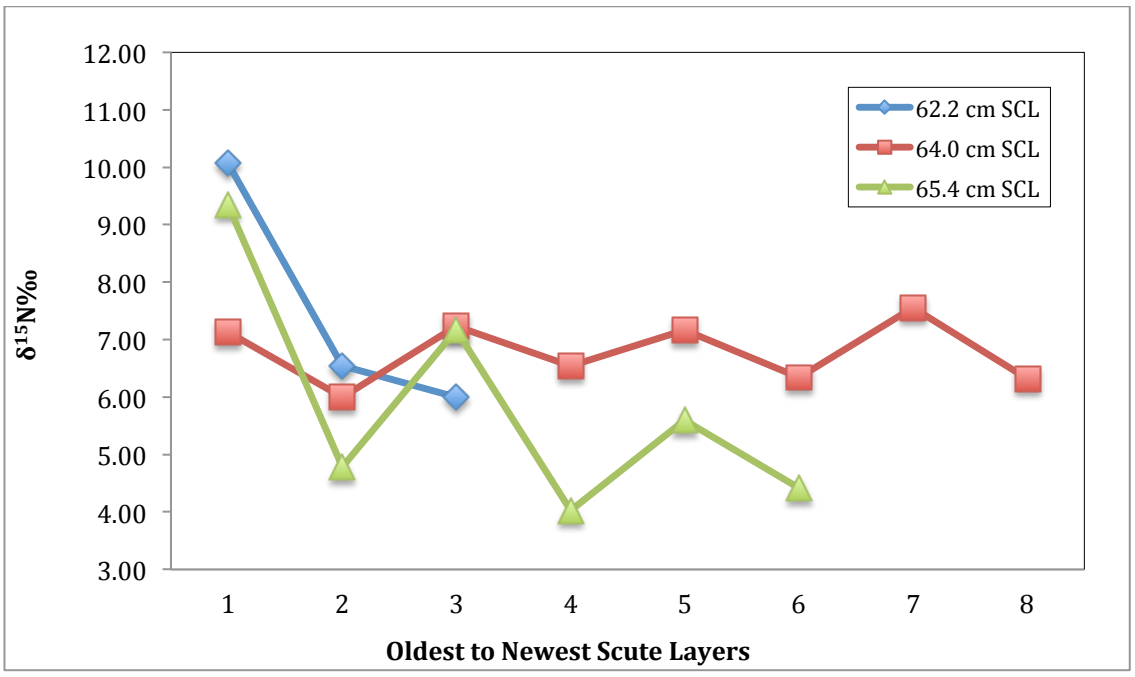


Figure 13. Isotope profiles of the (a) $\delta^{13}C$ values and (b) $\delta^{15}N$ values for scute tissue of the >55 cm SCL green sea turtle size class stranding along the middle Texas coast during 2007-2010.

Analysis of Stable Isotopes from Juvenile Green Turtles on the LTC. $\delta^{13}C$ values in newly synthesized tissue varied between each of the five size classes of green turtles from the LTC. Overall values were from -19.27 to -7.11‰. Mean $\delta^{13}C$ value for respective size classes (Fig. 14) was: 15-24.9 cm SCL: -17.03‰ ± 1.18, 25-34.9 cm SCL: -15.70‰ ± 3.76, 35-44.9 cm SCL: -8.70‰ ± 0.94, 45-54.9 cm SCL: -8.48‰ ± 0.74, and >55 cm SCL: -8.46‰ ± 0.91. In a similar mode, the scute $\delta^{15}N$ values across all size classes ranged from 6.06 to 16.21‰. Mean $\delta^{15}N$ value for each size class (Fig. 14) was: 15-24.9 cm SCL: 10.41‰ ± 2.81, 25-34.9 cm SCL: 10.39‰ ± 2.55, 35-44.9 cm SCL: 7.22‰ ± 0.64, 45-54.9 cm SCL: 8.06‰ ± 1.37, and >55 cm SCL: 8.12‰ ± 0.53. The $\delta^{13}C$ values among size classes sampled from the LTC varied significantly (Welch ANOVA $F_{4,14.766} = 21.087$, $p < 0.05$) as did $\delta^{15}N$ values (ANOVA $F_{4,12.691} = 5.305$, $p < 0.05$). $\delta^{13}C$ values of 15-24.9 and 25-34.9 cm SCL turtles differed significantly from those of other size ranges ($p < 0.05$). $\delta^{15}N$ values were significantly different between size class 25-34.9 and 35-44.9 cm SCL ($p < 0.05$). Distribution of isotope values of the newest tissue from all individuals (Fig. 15 a,b) illustrated changes in isotope concentrations with increasing turtle size.

Isotope Profiles of Juvenile Green Turtles from the LTC. Stable carbon and nitrogen isotope profiles for each of the size ranges illustrated changes in values with increasing size. Isotope profiles of the 15-24.9 cm SCL turtles (Fig. 16 a,b) exhibited enrichment of $\delta^{13}C$ and $\delta^{15}N$ values from the oldest tissue to the most recently synthesized. Results from the 25-34.9 cm SCL size

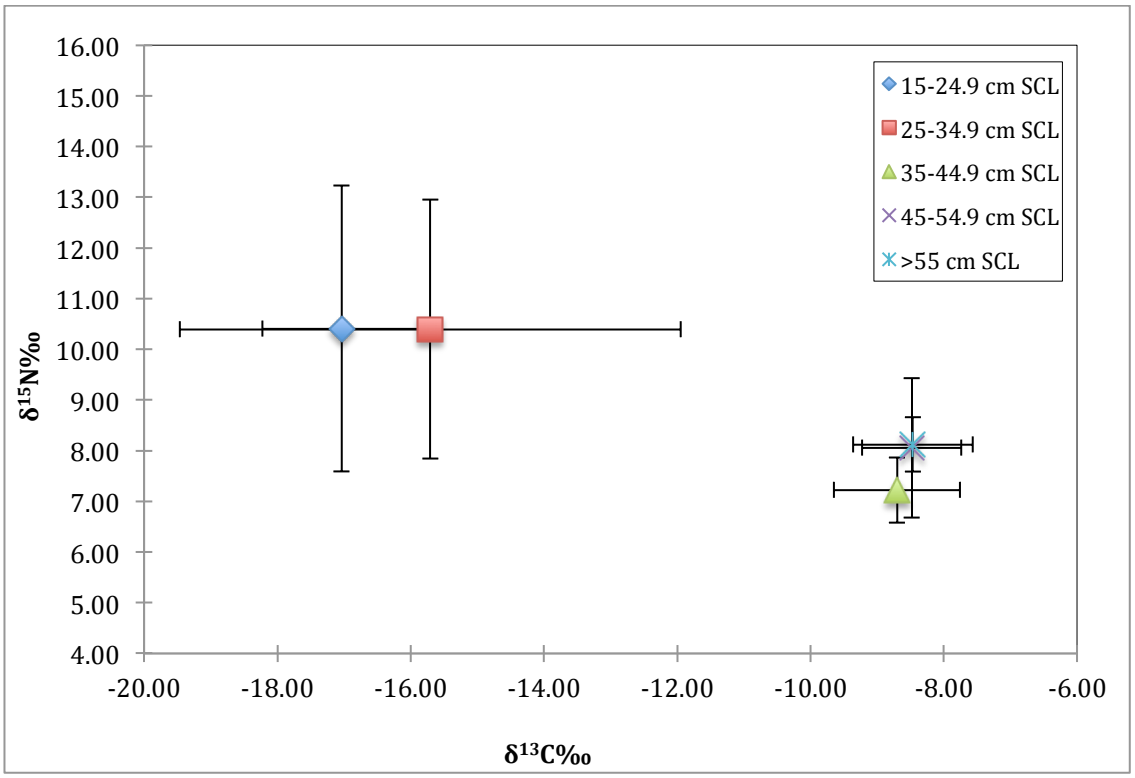


Figure 14. Mean $\delta^{13}C$ and $\delta^{15}N$ values (± SD) for the newest scute tissue of green sea turtles stranding along the lower Texas coast during 2007-2010.

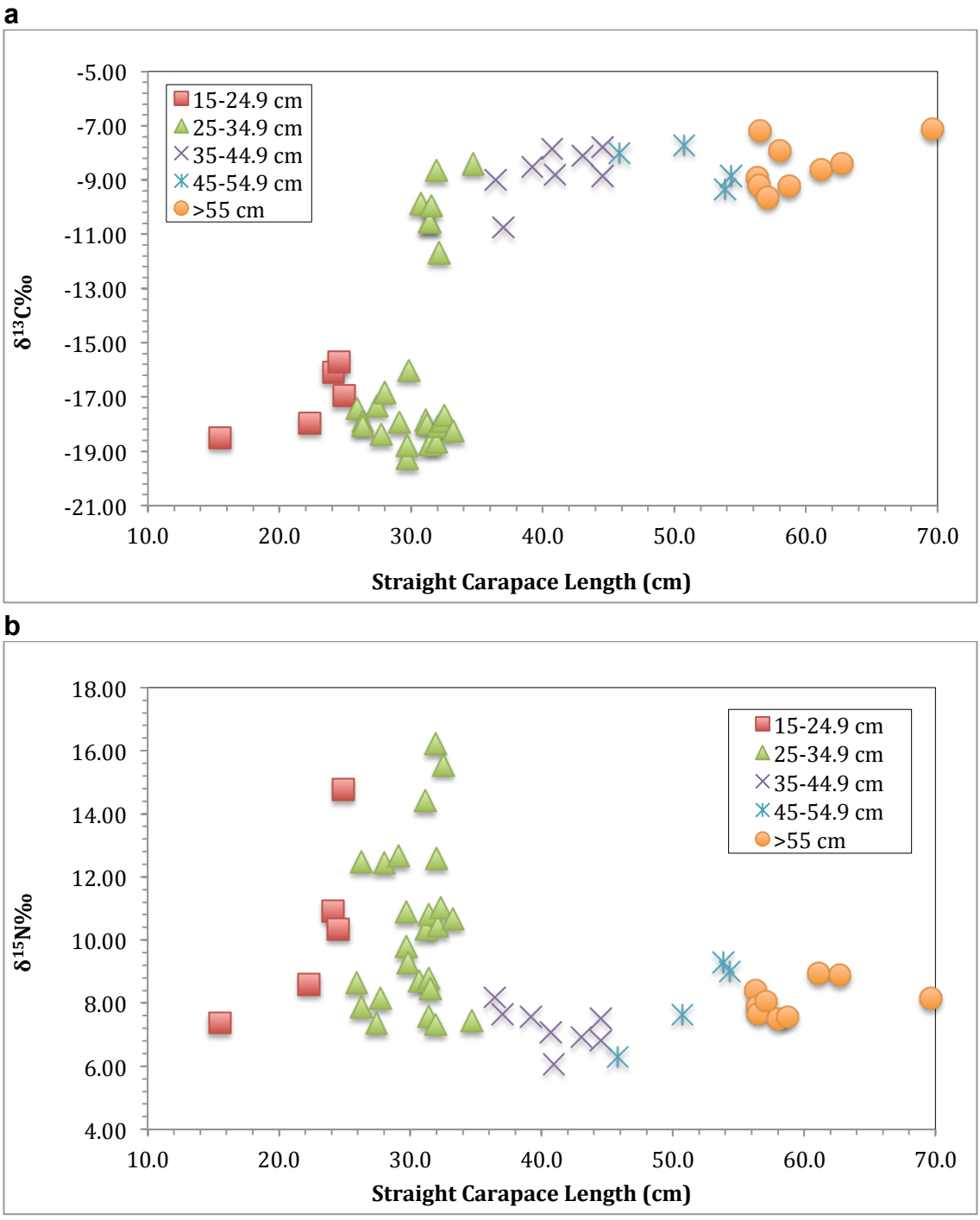
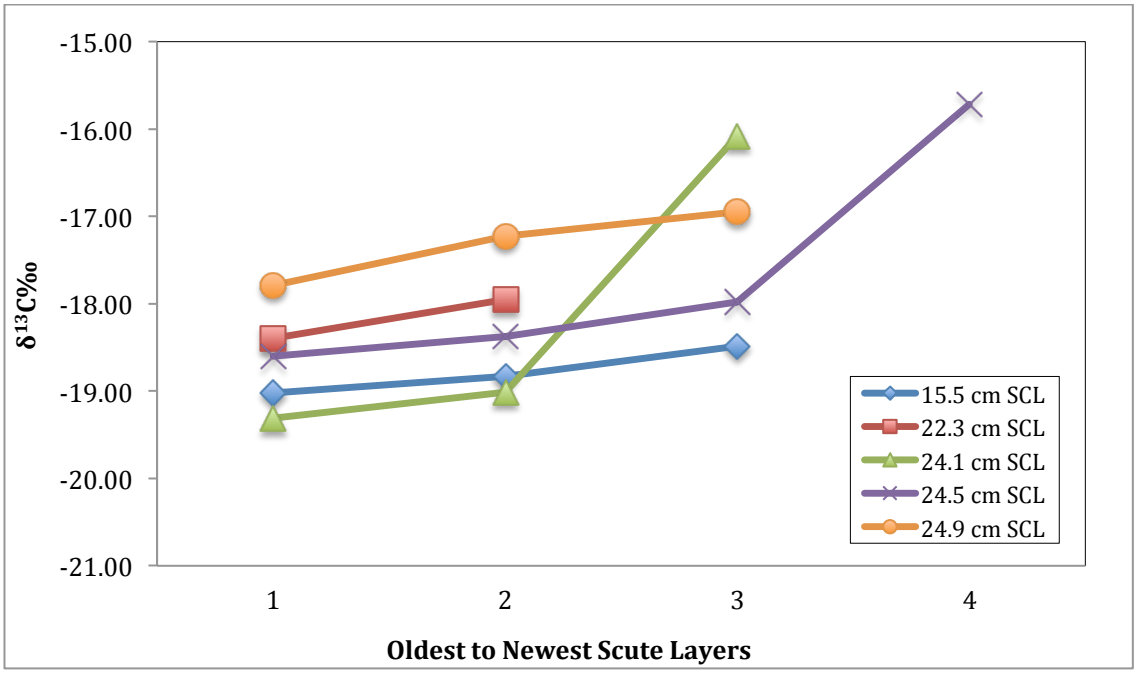


Figure 15. Distribution of (a) $\delta^{13}C$ values and (b) $\delta^{15}N$ values in newest scute tissue versus straight carapace length of green sea turtles stranding along the lower Texas coast during 2007-2010 (n = 51).

a



b

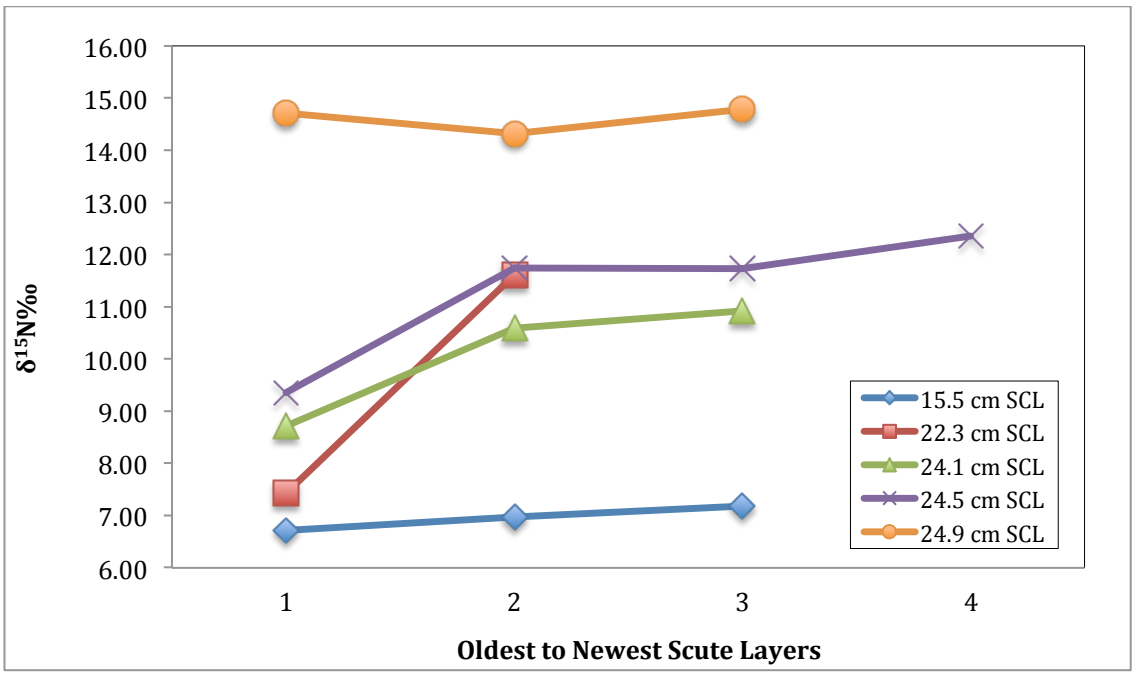
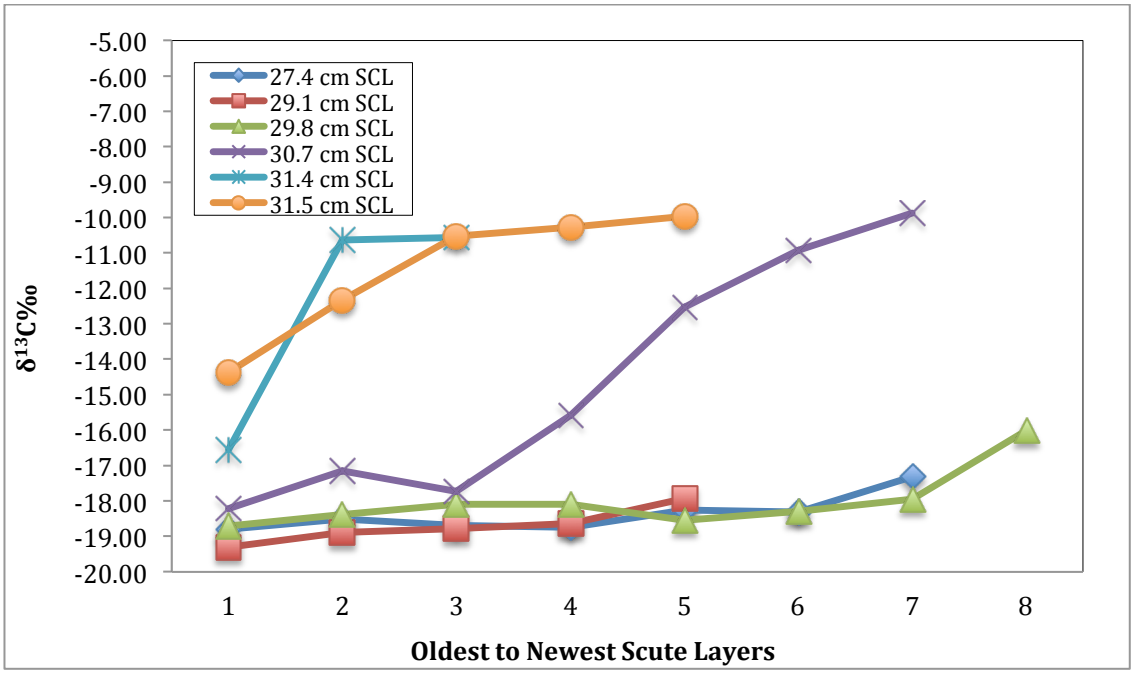


Figure 16. Isotope profiles of the (a) $\delta^{13}C$ values and (b) $\delta^{15}N$ values for scute tissue of the 15-24.9 cm SCL green sea turtle size class stranding along the lower Texas coast during 2007-2010.

class yielded some profiles with several layers of depleted $\delta^{13}C$ with little change in the isotope concentrations (Fig. 17a). Conversely, enriched $\delta^{13}C$ values were documented in the newest tissues of some turtle profiles within this size class. Similarly, $\delta^{15}N$ values were consistent in several successive layers of tissues of some profiles but displayed enrichment and then depletion in others (Fig. 17b). Values of the newest tissue layer of 35-44.9 cm SCL turtles were enriched in $\delta^{13}C$ and depleted in $\delta^{15}N$ compared to those of the oldest layers (Fig. 18 a,b). The oldest tissue layer of 45-54.9 cm SCL and >55 cm SCL turtles was depleted in $\delta^{13}C$ and enriched in $\delta^{15}N$ and just the reverse for the most recent layer (Fig. 19 a,b and Fig. 20 a,b). However, this was not the case for all turtles; some individuals had successive layers with isotope values that changed little in concentration.

Regional Comparison Analysis. No significant differences in $\delta^{13}C$ or $\delta^{15}N$ values were detected in the scute of 15-24.9 cm SCL turtles between the regions ($p > 0.05$). The $\delta^{13}C$ values were significantly different between the two areas for 25-34.9 cm SCL turtles, with the LTC demonstrating enriched values, $t(30.35) = -2.27$, $p < 0.05$. $\delta^{15}N$ values for 35-44.9 cm SCL turtles differed significantly between the two study areas, with the LTC assemblage exhibiting depleted nitrogen values, $t(4.32) = 2.85$, $p < 0.05$. No significant differences in $\delta^{13}C$ values or $\delta^{15}N$ values were detected in 45-54.9 cm SCL turtles between the regions ($p > 0.05$). $\delta^{15}N$ values for >55 cm SCL turtles differed significantly

a



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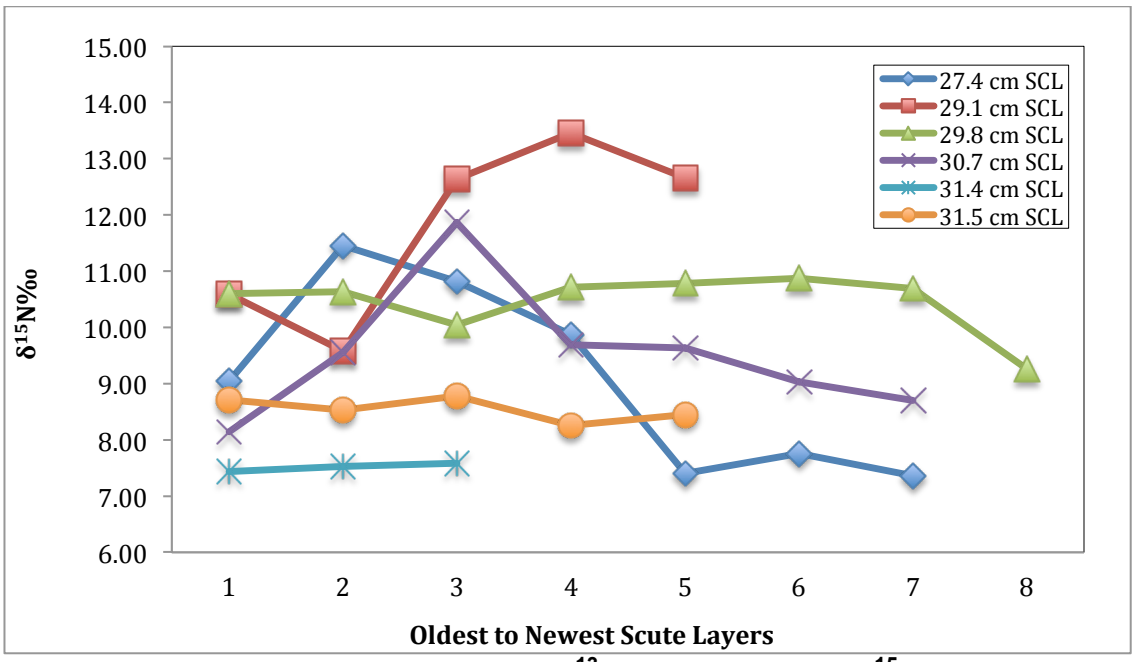
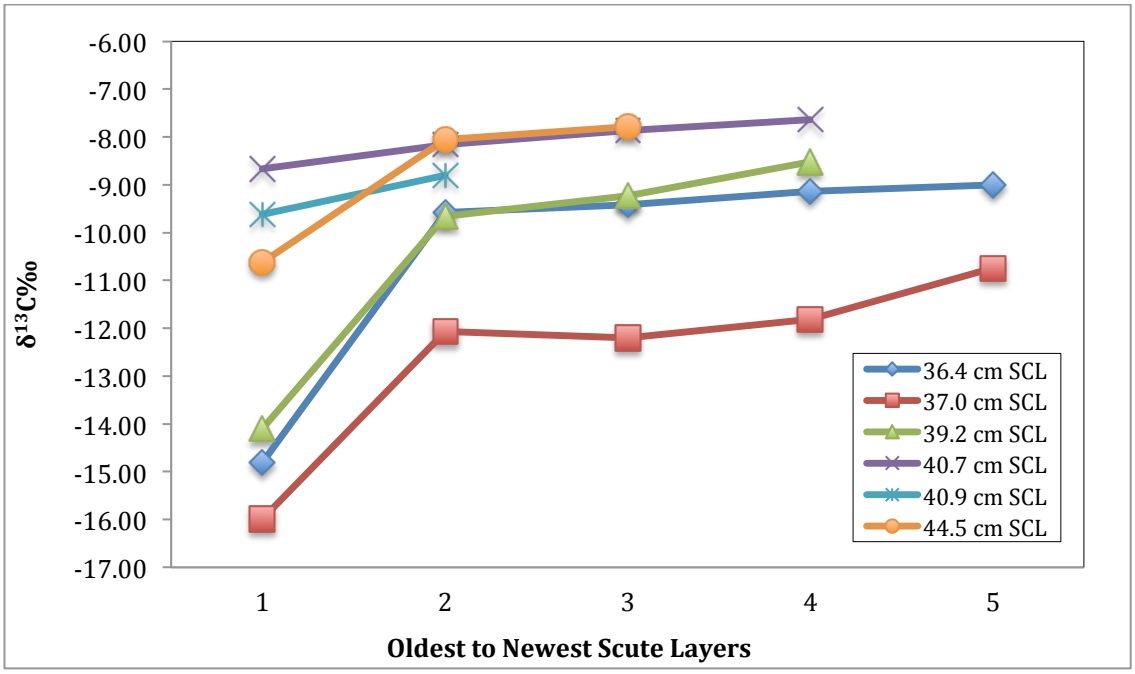


Figure 17. Isotope profiles of the (a) $\delta^{13}C$ values and (b) $\delta^{15}N$ values for scute tissue of the 25-34.9 cm SCL green sea turtle size class stranding along the lower Texas coast during 2007-2010.

a



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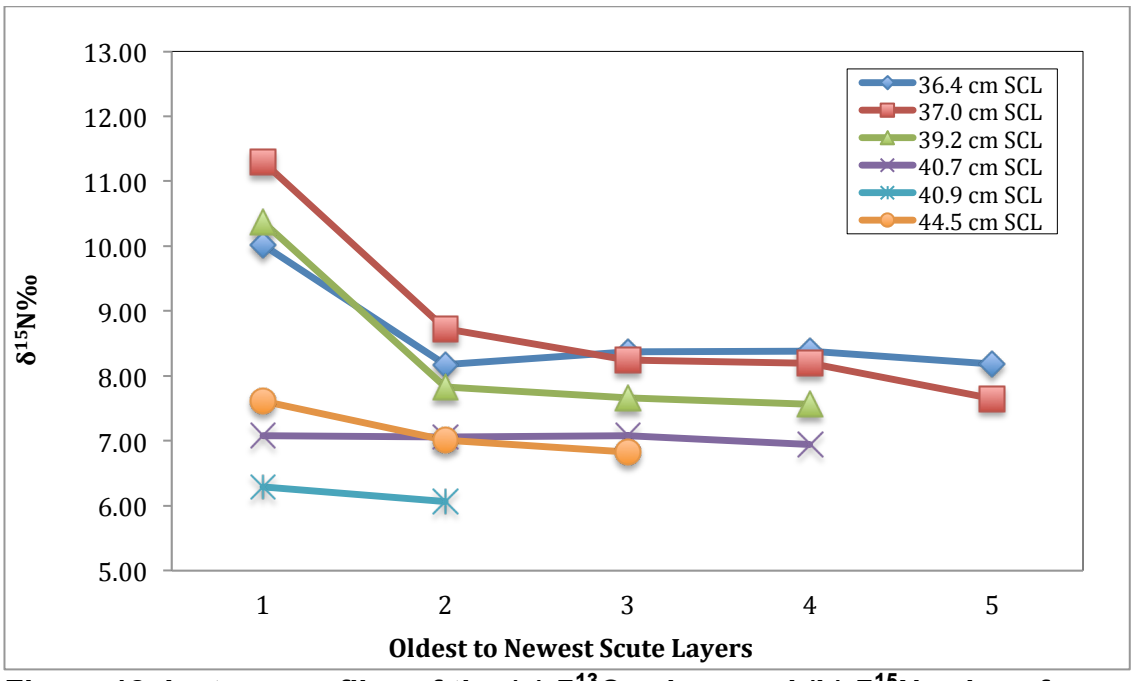
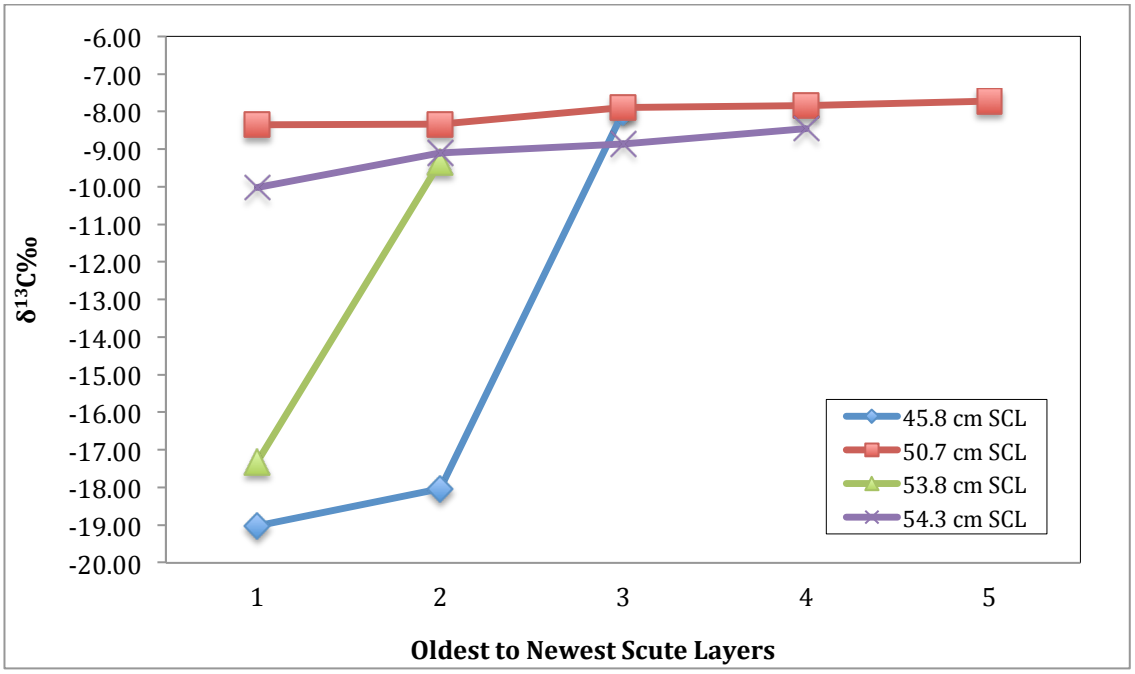


Figure 18. Isotope profiles of the (a) $\delta^{13}C$ values and (b) $\delta^{15}N$ values for scute tissue of the 35-44.9 cm SCL green sea turtle size class stranding along the lower Texas coast during 2007-2010.

a



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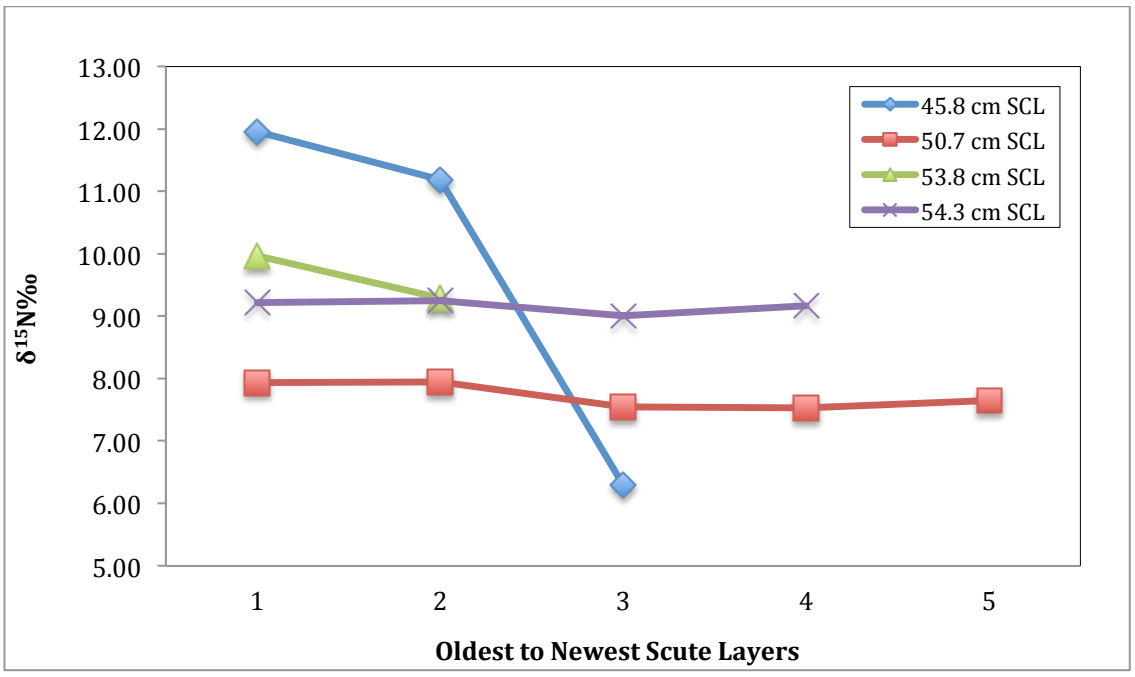
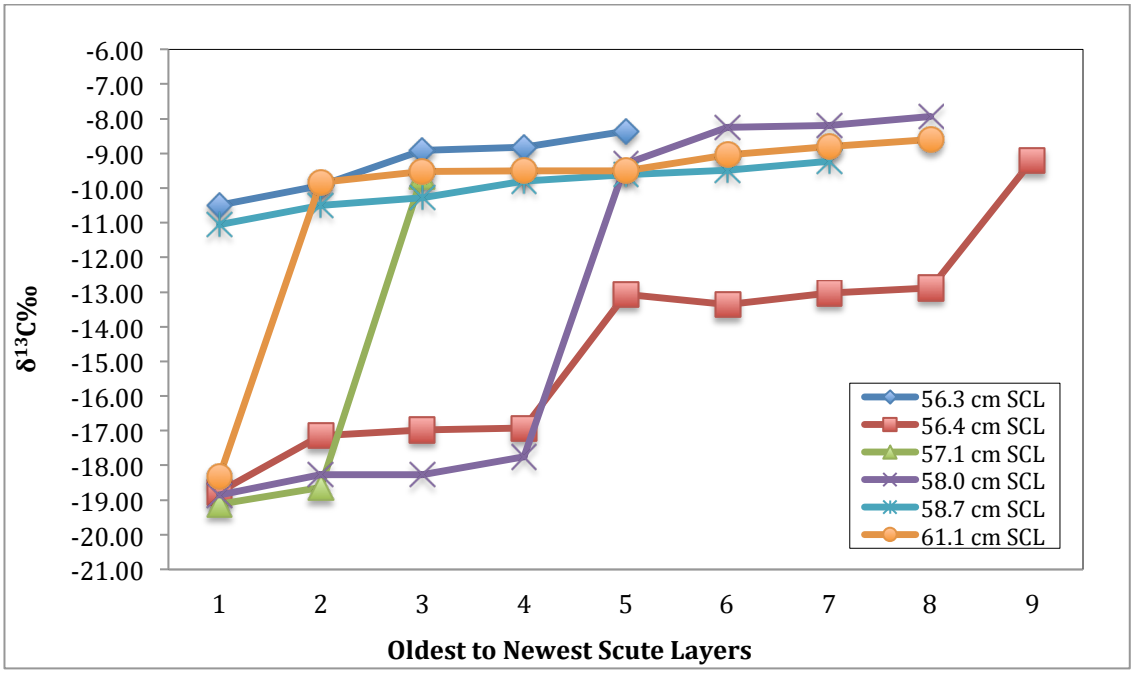


Figure 19. Isotope profiles of the (a) $\delta^{13}C$ values and (b) $\delta^{15}N$ values for scute tissue of the 45-54.9 cm SCL green sea turtle size class stranding along the lower Texas coast during 2007-2010.

a



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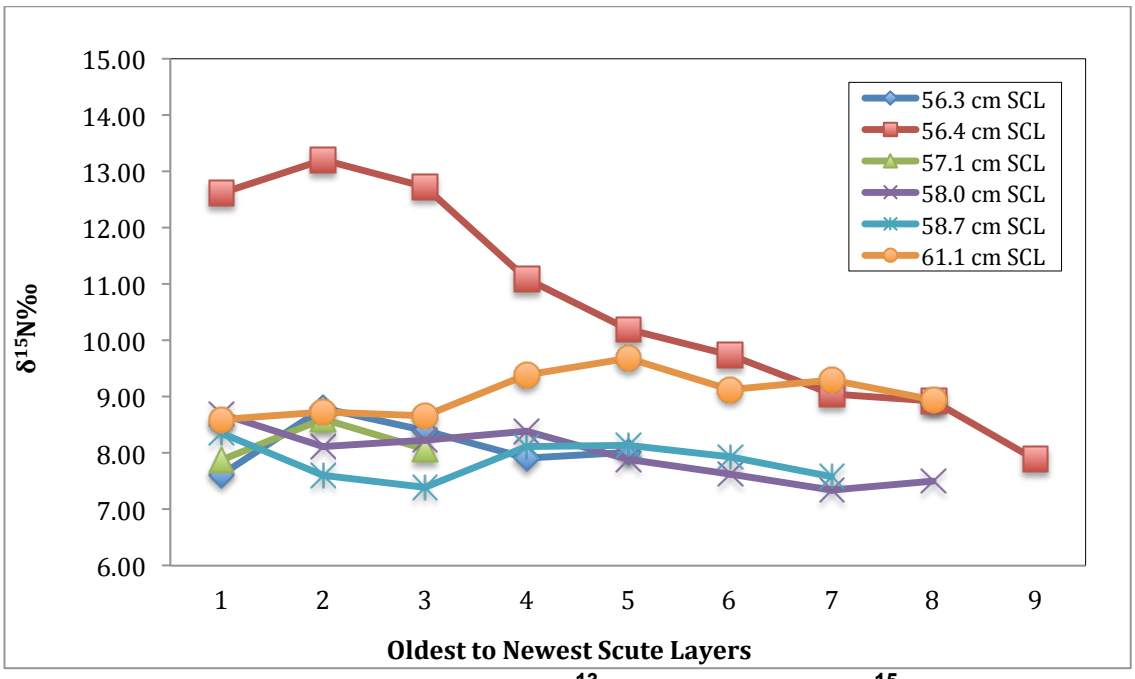

Figure 20. Isotope profiles of the (a) $\delta^{13}C$ values and (b) $\delta^{15}N$ values for scute tissue of the >55 cm SCL green sea turtle size class stranding along the lower Texas coast during 2007-2010.

between the MTC and LTC, with conspecifics from the MTC exhibiting depleted values, $t(10) = -5.76$, $p < 0.05$.

DISCUSSION

Analysis of Stable Isotopes from Juvenile Green Turtles on the MTC. Juvenile green turtles on the MTC exhibited ontogeny through multiple habitats with consequent diet changes. Scute tissue analysis of carbon and nitrogen stable isotopes revealed considerable variation between turtles >55 cm SCL and those for the other four classes examined from the MTC. Although not significant, a general trend of enrichment in $\delta^{13}C$ values with increasing size was observed across the five size classes. Similarly, nitrogen isotope values demonstrated a gradual depletion in value with increasing turtle size. Juvenile green turtles occupy the oceanic realm until nearshore recruitment at 20 to 25 cm SCL (Bjorndal & Bolten 1988). Similarly, in this study, only turtles <25 cm SCL exhibited newest tissue isotope values that indicate they were assimilating nutrients in the oceanic environment (Reich et al. 2007, Arthur et al. 2008). Oceanic juvenile green turtles consume a wide range of organisms, including amphipods, krill, copepods, barnacles, cnidarians and *Sargassum spp.* (Boyle & Limpus 2008). Foraging on these items elevated in $\delta^{15}N$ results in higher $\delta^{15}N$ values in their tissue (Wallace et al. 2009). Depleted $\delta^{13}C$ values detected in some of these turtles' scute tissue also suggest they occupied the oceanic realm (France 1995, Reich et al. 2007). Isotope profiles for some <20 cm SCL turtles demonstrated minimal change in the isotope values of successive layers of

tissue analyzed, with their $\delta^{15}N$ values consistent with those of omnivorous juvenile loggerheads occupying the oceanic environment (McClellan et al. 2010). However, a dichotomy in the $\delta^{13}C$ and $\delta^{15}N$ values existed in this size class, wherein some turtles exhibited an enrichment of $\delta^{13}C$ and $\delta^{15}N$ values compared to the isotope values of other counterparts. Specifically, the isotope profiles for >20 cm SCL turtles exhibited values in the newest tissue layers indicating a shift in habitat and diet from the oceanic stage had occurred. Reich et al. (2008) reported the rate of incorporation of nitrogen and carbon into juvenile loggerhead tissue was not equal with nitrogen incorporation more rapid than that of carbon (Reich et al. 2007). Therefore, it is conceivable that the considerably enriched $\delta^{15}N$ values of some 15-24.9 cm SCL turtles denotes they had recruited to and were foraging within nearshore waters but their $\delta^{13}C$ values had not changed considerably to reflect the new habitat occupied. Reported isotope values for algae consumed by juvenile green turtles at Texas jetties (Gorga 2010) (L. N. Howell, person. observ) include *Gelidium* spp. ($\delta^{13}C$ -20.39‰ ± 0.17 SD, $\delta^{15}N$ 10.07‰ ± 0.07 SD) and *Ulva spp.* ($\delta^{13}C$ -17.08‰ ± 0.03 SD, $\delta^{15}N$ 8.52‰ ± 0.12 SD) (Fig. 21). Considering the discrimination factors for juvenile sea turtle tissue, $\Delta_{dt}\,\delta^{13}C$: + 0.17 ‰ and $\Delta_{dt}\,\delta^{15}N$: + 2.92 ‰ (Seminoff et al. 2006), it is presumed that the turtles had been foraging on macroalgae on jetty structures. Enriched $\delta^{13}C$ and $\delta^{15}N$ values in 25-34.9 cm SCL turtles compared to those of oceanic stage turtles also indicates this size range of turtles had consumed predominantly macroalgae in jetty habitat. The broad range of $\delta^{15}N$ values for

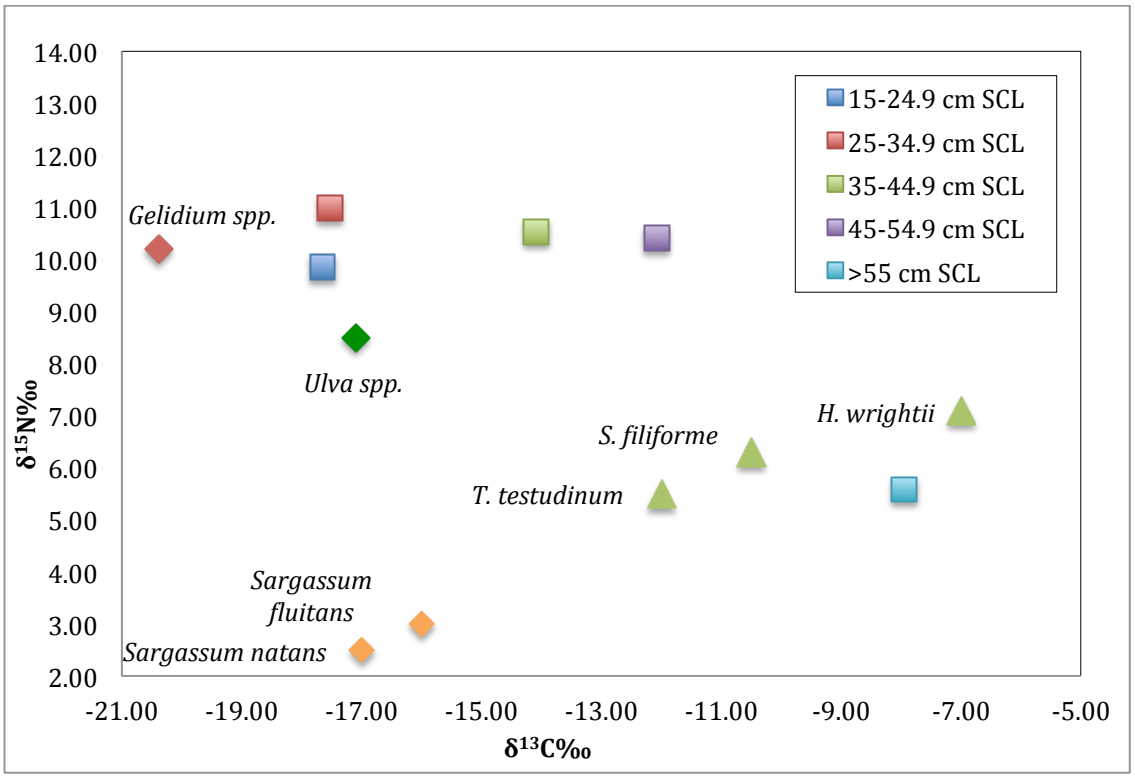

Figure 21: Mean $\delta^{13}C$ and $\delta^{15}N$ values for all size classes of green sea turtles stranding along the middle Texas coast during 2007-2010. ■ = turtle size class ◆ = mean value for macroalgae species consumed by green turtles Δ = mean value for seagrass species consumed by green turtles.

this size range of turtles may suggest divergent foraging tactics. Elevated $\delta^{15}N$ values in birds have been attributed to periods of fasting (Hobson 1993) as well as overall diet quality and protein content. However, turtles utilized in this study were all noted to be in good health, with no abnormalities detected during gross necropsy. Enriched $\delta^{15}N$ values reported herein are within previously reported ranges ($\delta^{15}N$ of 8.6 to 16.9‰) for turtles presumed to be foraging on enriched $\delta^{15}N$ plant material and animal matter (Hatase et al. 2006, Arthur et al. 2008, Lemons et al. 2011). Therefore, turtles within this size range are likely consuming animal matter and macroalgae differentially, resulting in divergent $\delta^{15}N$ values. Residency within a transitional habitat in this life stage of a green turtle could result in analogous isotope values from the oldest tissues to the newest tissue of an individual (Reich et al. 2007). The minimal change of $\delta^{13}C$ values through uninterrupted layers of scute examined for some individuals may be indicative of long-term habitat occupancy.

Contrasting $\delta^{13}C$ and $\delta^{15}N$ isotope values existed for 35-44.9 cm SCL turtles (n=5). Isotope values for the newest synthesized tissue of two turtles were indicative of foraging within the seagrass beds; their isotope profiles demonstrated multiple shifts with stepwise enrichment of $\delta^{13}C$ and depletion of $\delta^{15}N$. Conversely the remaining size class profiles exemplified only one shift, oceanic to the jetty habitat, with no subsequent transference to seagrass beds. $\delta^{13}C$ values of new green turtle recruits to seagrass pastures do not quickly approach the $\delta^{13}C$ values of long-term residents (Arthur et al. 2008), which

consequently allows distinction between recent and long-term inhabitants. Therefore, it is conceivable that >35 cm SCL turtles with $\delta^{13}C$ and $\delta^{15}N$ values indicative of jetty occupancy may be instead recent recruits to seagrass beds. Gorga (2010) used $\delta^{13}C$ and $\delta^{15}N$ values to determine turtles >35 cm SCL along the MTC were seagrass occupants. The divergence of isotope values for the 35-44.9 cm SCL size range could also suggest MTC turtles exhibit two different foraging strategies. Some larger turtles, possibly driven by limited forage availability in MTC bay systems (TPWD 1999), may inhabit jetty habitat for extensive periods and display opportunistic foraging habits along those structures. The limited number (n=5) of 35-44.9 cm SCL turtles analyzed mandates caution when inferring trends for this size class.

Mean $\delta^{13}C$ and $\delta^{15}N$ values of 45-54.9 cm SCL turtles suggest this size class is occupying jetty localities but examination of individual isotope profiles revealed a dichotomy in isotope values across the size class. Two individual's isotope profiles clearly exhibited the shift from jetty habitat to seagrasses while the third profile did not. Tissue, such as scute, with a slower isotope turnover rate (Reich et al. 2008) subsequently reflect a longer-term dietary average (Hobson & Clark 1992). Additionally, Cardona et al. (2010) reported that juvenile green turtles in the Mediterranean did not demonstrate a sudden change in isotope concentration following recruitment to seagrass beds but instead exhibited a gradual adjustment in isotope values. Therefore, it is possible the third individual had recently transitioned to seagrass beds and consequently the

isotope values present in the recent tissue layer were an average of two different habitats occupied and diets consumed. The limited number (n=3) of 45-54.9 cm SCL turtles analyzed dictates caution when interpreting trends for this size class.

Intermediate developmental stages in nearshore areas prior to recruitment of <45 cm SCL juveniles to seagrass pastures have been documented in in the Atlantic (Mendonca & Erhart 1982, Henwood & Ogren 1987) and for 40-65 cm SCL conspecifics in the Pacific (Arthur et al. 2008). Furthermore, in-water research in Texas has documented 40-59.9 cm SCL turtles (n <10) residing within the jetty zone (Shaver 2000). As such, some turtles (35-55 cm SCL) in the MTC may occupy this jetty habitat longer foraging on macroalgae and invertebrates on the granite structures prior to transitioning to seagrass beds.

Significantly enriched $\delta^{13}C$ and depleted $\delta^{15}N$ values for all >55 cm SCL turtles (n=3) along the MTC suggests they were occupying a different environment than smaller counterparts were. Mean isotope values of seagrass species from the MTC were *T. testudinum:* $\delta^{13}C$ 12.03‰ ± 0.16 SD, $\delta^{15}N$ 5.59‰ ± 0.11 SD and *S. filiforme:* $\delta^{13}C$ -10.82‰ ± 0.14 SD, $\delta^{15}N$ 6.32‰ ± 0.23 SD (Fig. 22). Results of stable isotope analysis of carbon and nitrogen in samples from the largest size class of turtles in this study indicate that turtles >55 cm SCL limit their foraging to seagrass beds. Seagrass spp. have been documented as a dominant diet item in green sea turtle populations in the Caribbean (Mortimer 1981, Bjorndal 1982), in Queensland, Australia (Arthur et al. 2009), the

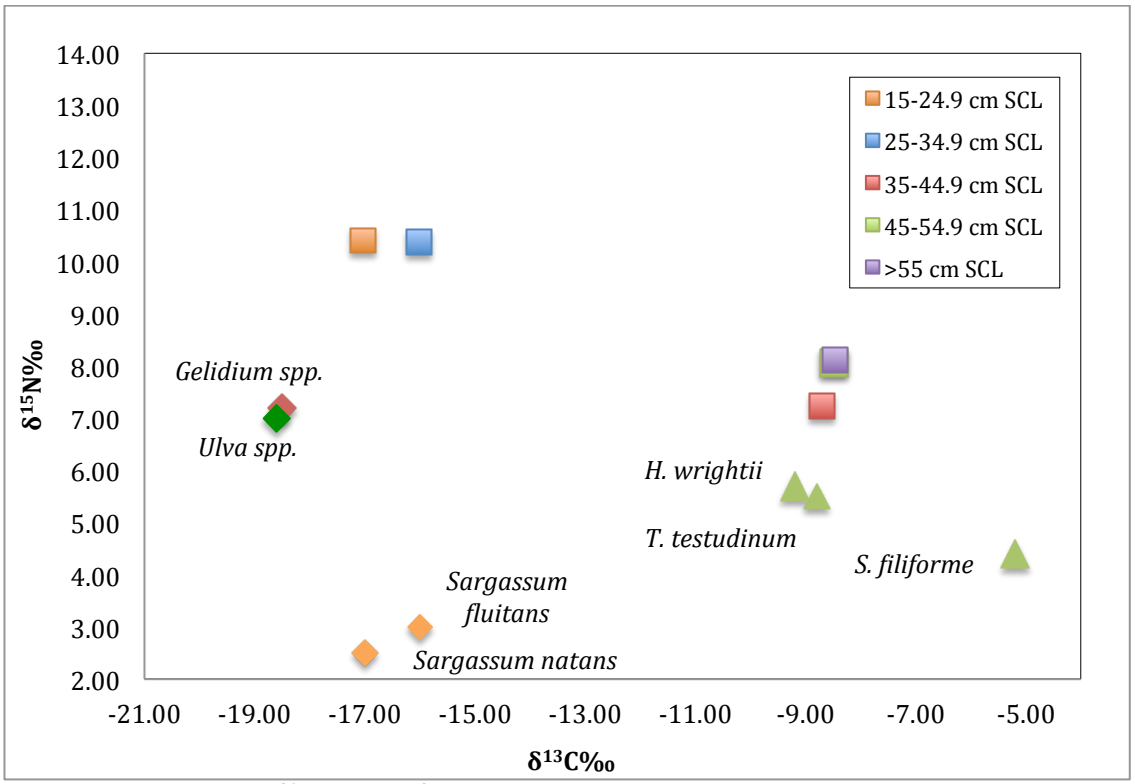

Figure 22: Mean $\delta^{13}C$ and $\delta^{15}N$ values for all size classes of green sea turtles stranding along the lower Texas coast during 2007-2010. ■ = turtle size class ◆ = mean value for macroalgae species consumed by green turtles Δ = mean value for seagrass species consumed by green turtles.

Atlantic (Mendonca 1983), as well as in Texas' Laguna Madre (Coyne 1994). Isotope profiles of two >55 cm SCL turtles demonstrate the shift in habitat and diet with the enrichment of $\delta^{13}C$ values and depletion of $\delta^{15}N$ in the newest tissue. However, $\delta^{13}C$ and $\delta^{15}N$ values of the third turtle, 64.0 cm SCL, were relatively constant and did not exemplify any recent shifts in habitat indicating long-term seagrass bed residency. Several studies have reported similar enriched $\delta^{13}C$ values for large juvenile green turtles resident within seagrass-dominated bays (Reich et al. 2007, Arthur et al. 2008, Cardona et al. 2009). Findings reported herein, despite limited sample size, confirm that seagrasses constitute the main diet component of >55 cm SCL juvenile turtles.

Isotope values from the continuous tissue layers for all green turtles from the MTC generally describe a pattern of changing isotope values as conspecifics shift in habitat occupation and diet consumed with increased size. $\delta^{13}C$ values clearly illustrate a size-based habitat segregation occurring in juvenile turtles from the MTC. Oceanic and jetty environments are occupied by turtles < 25 cm SCL; >25 cm SCL counterparts reside at jetty habitat; and >35 cm SCL conspecifics inhabit inshore seagrass pastures. Failure of seagrass bed occupancy to be characteristic of all 35 to 54.9 cm SCL turtles from the MTC was an exception to this trend.

Analysis of Stable Isotopes from Juvenile Green Turtles on the LTC. Several juvenile green turtle size-based transformations were documented for the LTC through analysis of ^{13}C and ^{15}N present in scute tissue. Significant

differences were observed in the isotopic values of $\delta^{13}C$ and $\delta^{15}N$ among three size classes: 15-24.9, 25-34.9 and 35-44.9 cm SCL. Turtles in the 15-24.9 cm SCL size class exhibited significantly higher $\delta^{15}N$ values ($p < 0.05$) that exemplified foraging at a trophic level parallel to what has been well documented in oceanic stage loggerheads (Wallace et al. 2009). Depleted $\delta^{13}C$ values, analogous to values for MTC 15-24.9 cm SCL turtles, suggest most of these conspecifics were from the oceanic realm. Small size at recruitment to nearshore waters has been observed in the western Atlantic, where Bjorndal and Bolten (1988) reported ≥ 20 cm SCL turtles entering neritic benthic foraging areas. However, individual isotope profiles of newest tissue layers in some <20 cm SCL turtles were enriched in $\delta^{15}N$ and $\delta^{13}C$. Isotope enrichment in the newest tissue layer indicates these turtles were not in the oceanic stage but instead were nearshore recruits. These results are similar to those observed for 15-24.9 cm SCL turtles from the MTC that demonstrated recruitment to jetty localities.

Oceanic juvenile green turtles recruit to protected coastal areas rich in marine algae or seagrasses and, after this initial residency in early developmental sites, migrate to other locations as larger juveniles (Musick & Limpus 1997, Zug & Glor 1998). Developmental habitat shift with subsequent diet change is evident in the isotope profiles of <35 cm SCL turtles. Macroalgae are enriched in $\delta^{15}N$ and depleted in $\delta^{13}C$ relative to counterpart values for seagrasses, with this difference partially explained by the degree of fractionation

of 13C/12C during photosynthesis (Raven et al. 1995). The majority of turtles within the 25-34.9 cm SCL size range had newest tissue isotope values enriched in $\delta^{15}N$ and depleted in $\delta^{13}C$, thus signifying they were foraging on nearshore macroalgae. This foraging strategy is similar to that reported for turtles in the Pacific exhibiting a transitional stage of macroalgae and mangrove consumption prior to foraging on seagrasses (Arthur et al. 2008). However, a clear separation in the $\delta^{13}C$ values of 25-34.9 cm SCL turtles existed generating two distinct groups that were evident by a paucity of $\delta^{13}C$ values between these two groups. Several >30 cm SCL turtles had significantly enriched $\delta^{13}C$ and depleted $\delta^{15}N$ values, signifying they had been foraging within seagrass beds. A seagrass-dominated diet has been previously observed in stomach lavage samples from >30 cm SCL turtle from this region (Coyne 1994). Therefore, it is probable turtles between 30 and 35 cm SCL transition to seagrass beds on the LTC.

The transition from oceanic stage to developmental jetty habitat and then to seagrass beds was clearly exemplified within >35 cm SCL turtles by the variance in isotope profile values from their oldest to newest tissue. The ontogeny of the dietary shift from jetty macroalgae to inshore seagrass beds in LTC juvenile green turtles is similar to the change in isotope values reported for green turtle recruits in the Caribbean (Reich et al. 2007) and eastern Australia (Arthur et al. 2008). A significant change in the mean carbon isotope value occurred from 25-34.9 cm SCL ($\delta^{13}C$ -15.70‰ ± 3.76) to 35-44.9 cm SCL ($\delta^{13}C$ -8.70‰ ± 0.94) turtles, illustrating a definitive habitat and diet transition. Enriched

$\delta^{13}C$ values and depleted $\delta^{15}N$ values signified all >35 cm SCL LTC turtles had been foraging upon inshore seagrass pastures. Furthermore, no significant differences between $\delta^{13}C$ and $\delta^{15}N$ were detected between the newest tissue values of the three largest size classes. Unidirectional shifts in habitat and diet occurred in juvenile turtles from the LTC, as evidenced by the isotope profiles for these largest size classes. Size-based habitat segregation is substantiated by the primary nutrients assimilated within LTC turtles >35 cm SCL being derived from seagrass beds.

Regional Comparison. The two regions of the Texas coast investigated in this study did not exhibit equivalent juvenile green turtle size-based habitat residency. Isotope values of scute samples from 15-24.9 cm SCL turtles were not significantly different between regions. Green turtles are considered occupants of the oceanic environment or recent nearshore recruits at 20-45 cm SCL (Bjorndal 1997, Musick & Limpus 1997). As previously discussed for both regions, this size range consists of both oceanic residents and recent recruits; consequently, this study's results conclude that green turtles are recruiting to neritic waters in Texas at <24.9 cm SCL. In contrast, $\delta^{13}C$ values were significantly different ($p > 0.05$) between the two areas for 25-34.9 cm SCL turtles, with LTC counterparts demonstrating enriched $\delta^{13}C$ values. Latitudinal differences in turtle foraging locations have been suggested to produce variations in isotope values of tissue from adult loggerhead turtles (Reich et al. 2010). Some of the dissimilarity in $\delta^{13}C$ values within the 25-34.9 cm SCL size

class could be due to latitudinal differences, MTC (29.0°N) and LTC (26.0°N). However, given the similarity in $\delta^{13}C$ values of turtles that are seagrass bed recruits in both regions, it is not likely a significant factor in the variance. In-water entanglement studies have captured <35 cm SCL turtles in the seagrass beds of the LTC (Landry et al. 1992, Coyne 1994). Consequently, the disparity in isotope values of turtles from these two regions is probably a result of more LTC 25-34.9 cm SCL inhabitants present inshore at seagrass beds while the majority of MTC counterparts reside at jetty locales as their depleted $\delta^{13}C$ values validate. The largest concentration of turtles residing along the Texas coast has been documented in the lower Laguna Madre (Hildebrand 1982, Shaver 2000). In addition to the other variables discussed previously (forage material and abundance, nutritional content, and temperature), the observed differences between the two regions could also result from competition for forage among turtles at LTC jetty structures, subsequently driving some <35 cm SCL turtles to abundant widespread food resources in adjacent bays.

Discharge of nutrients from agriculture processes, industrial operations, and sewage treatment has led to a noticeable increase in nitrogen export to nearshore coastal areas (Howarth et al. 2002). Elevated $\delta^{15}N$ values observed in the tissues of jetty turtles from both regions could likewise be partially due to nitrogen loading in the navigable waterways protected by jetty structures. Additionally, the minimal change of $\delta^{13}C$ values through uninterrupted layers of scute examined for some individuals may be indicative of long-term jetty habitat

occupancy.

Sea turtles that have been in limited resources or low temperatures demonstrate compensatory growth once in improved conditions (Bjorndal et al. 2003), so it is necessary to be cognizant of individual growth differences within a size class. Nonetheless, growth estimates for juvenile green turtles in south Texas are 5.26 cm/year based on recaptures of 22.2 to 55.8 cm SCL turtles (Coyne 1994). Combining growth evidence with results from this study indicates turtles reside in the jetty habitat a minimum of 2 - 3 years before recruiting to seagrass beds.

Isotopic analyses confirmed a regional difference in $\delta^{15}N$ values of scute samples from 35-44.9 cm SCL turtles. Depleted $\delta^{15}N$ in LTC samples indicates these conspecifics had not been consuming macroalgae within the jetty habitat, as enriched $\delta^{15}N$ values demonstrated their regional counterparts had been. Consequently, these results further support data suggesting MTC 35-44.9 cm SCL individuals resided at the jetty habitat, a larger size than LTC turtles. No regional differences were observed in the $\delta^{13}C$ or $\delta^{15}N$ values of 45-54.9 cm SCL turtles; these results may be influenced by limited sample size (total n=7). As previously considered for MTC 45-54.9 cm SCL turtles, there was a divergence in isotope values that implied both habitats are occupied by turtles of this size class. In contrast, isotope values for all LTC 45-54.9 cm SCL turtles indicates foraging within seagrass beds only. Additional samples within this size range are necessary to accurately determine regional differences in foraging

strategy.

Elevated $\delta^{15}N$ values in the scute of >35 cm SCL turtles along the LTC compared to those for MTC seagrass bed recruits might be partially due to anthropogenic nitrogen loading from pollution (Carmichael et al. 2004) as noted in isotope values of turtles residing in urbanized areas (Gorga 2010, Lemons et al. 2011). However, assimilation of an invertebrate diet resulted in enriched $\delta^{15}N$ values of ontogenetic juvenile green turtles in the Mediterranean and northwestern Africa (Cardona et al. 2009, 2010). It is plausible turtles in the LTC are supplementing their seagrass diet with animal matter, with subsequent assimilation of that diet yielding enriched $\delta^{15}N$ values. The abundance of seagrasses in the LTC may result in a more clearly defined juvenile turtle size-based habitat and diet choice by >35 cm SCL compared to the jetty to seagrass bed transition exhibited by turtles from the MTC. Regardless of sampling region, isotope values reported herein for the dead turtles utilized were analogous to isotope values from a study of live, in-water netted Texas green turtles exhibiting an ontogenetic transition in diet and habitat (Gorga 2010).

CHAPTER IV

SUMMARY AND CONCLUSIONS

Multiple shifts in diet and habitat use by juvenile green sea turtles along the Texas coast were characterized through integration of stomach content and stable isotope analyses for 114 stranded turtles collected during 2007-2010. Examination of relatively undigested stomach contents was beneficial in discerning size-based differences in foraging behavior of juvenile conspecifics, as well as establishing a baseline of recent diet items consumed by Texas' green turtles. Stomach content analysis of juvenile turtles <25 cm SCL yielded a diet of oceanic items or macroalgae, while that for 25-34.9 cm SCL turtles revealed a primary dependence on macroalgae for MTC turtles and seagrass for LTC turtles. Seagrasses were the principal diet item of >35 cm SCL turtles, except for the MTC 45-54.9 cm SCL class (n=3), where macroalgae and animals dominated the diet. The regional difference observed in foraging habits suggests that some individuals may be specialists in a limiting environment. Although gut content analysis provided detailed information on forage material consumed, this traditional method of food habit analysis yielded data only for the most recent foraging events, a small window of time in the animal's overall diet history. In contrast, stable isotope analysis of $\delta^{13}C$ and $\delta^{15}N$ values of scute tissue revealed long-term diet, as well as habitat occupancy of juvenile turtles. Furthermore, time-integrated transitions in the diet and habitat of Texas' juvenile

green turtles were also illustrated with the stable isotope analysis of sequential layers of scute from individual turtles. Depleted $\delta^{13}C$ values and enriched $\delta^{15}N$ values suggest that <25 cm SCL turtles had recently inhabited oceanic waters. Enriched $\delta^{13}C$ and $\delta^{15}N$ values present in scute tissue of MTC <55 cm SCL and LTC <35 cm SCL turtles were indicative of residency at jetty habitat. Similar isotope values in successive layers of green turtle tissue from both regions suggests jetty habitat residency for an extended period of time prior to seagrass bed recruitment. Seagrass bed occupancy was exhibited by enriched $\delta^{13}C$ values and depleted $\delta^{15}N$ values in >30 cm SCL turtles from both regions. Evident in this analysis is that post-oceanic green turtles recruit to the jetty region at ~ 20 cm SCL, with most inhabiting this area up to 35 cm SCL before migrating and establishing residency in seagrass beds. This is the first study to integrate examination of stomach content from several size classes of green sea turtles with analysis of stable isotopes in their tissue. The combination of these two techniques provided an assessment of the efficacy of isotope analyses in documenting diet and habitat shifts. Stomach content analysis revealed the most recent diet consumed within the habitat occupied, whereas stable isotope analysis provided a time-integrated synopsis of the multiple transitions in diet and habitat. Thus, the results of this study highlight the significance of incorporating stable isotope analysis with stomach content examination in studies of marine-turtle foraging ecology.

Long-term occupation of both jetty and seagrass habitats by juvenile green turtles in Texas was exemplified in this study. Marine turtles inhabiting these environments can be impacted from dredge operations, boat strikes, incidental fisheries capture, fishing line entanglement, hypothermic stunning during cold weather events, ingestion of marine debris and harmful algal blooms. Results from this work on the foraging dynamics of green turtles can be utilized by management agencies to enhance regulations and protection measures, thus strengthening programs aimed at protection of this threatened species and the habitats on which it depends. Size-related variation in sea turtle foraging activities necessitates integrated management strategies that minimize impacts to juveniles in jetty and seagrass habitats. For instance, based on the size range of turtles residing inshore, gear modifications in commercial fisheries could be implemented as necessary to reduce incidental take thus providing increased protection of this threatened species. Additionally, it is essential to ensure better management of the critical seagrass beds that are fundamental to the growth and survival of this exponentially increasing green turtle population that will eventually recruit to the breeding supply.

Although this research provided valuable knowledge on green turtle foraging ecology in Texas, future studies should involve stable isotope analysis of known diet items for incorporation into isotope modeling for long-term diet inferences. Especially important is to establish the stable isotope values of epiphytic algae on seagrasses to determine if turtles within seagrass beds are

assimilating nutrients from both food items. Determining the nutritive value of seagrasses and macroalgae within respective habitats in both regions could provide insight on the observed regional size class differences. Increasing population trends in green turtle assemblages along the middle and lower Texas coast suggest a subsequent rise in the number of older juveniles and subadults that reside in seagrass habitat. Therefore, examining the nutrition requirements of green turtles within seagrass beds is vital as these large turtles become mature and part of the breeding stock. Finally, it is recommended that tissue samples continue to be collected for stable isotope analysis to monitor any potential baseline shifts as this population continues to show exponential growth and as the habitat changes due to urban development, pollution, and climate change.

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